UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
AGRICULTURAL SCIENCES
Vol. 3, No. 11, pp. 283-368, plates 25-42, 9 text figures April 4, 1919

AN INVESTIGATION OF THE ABNORMAL SHEDDING OF YOUNG FRUITS OF THE WASHINGTON NAVEL ORANGES

BY
J. ELIOT COIT AND ROBERT W. HODGSON

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY

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AN INVESTIGATION OF THE ABNORMAL SHEDDING OF YOUNG FRUITS OF THE WASHINGTON NAVEL ORANGE*

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Introduction

The genus *Citrus* is undoubtedly of tropical origin. Alphonse de Candolle, after much investigation of historical and philological data, concludes that the feral range of the sweet orange is South China, Cochin China, Java, and Sumatra, with a possible extension into India, which regions are classed ecologically as tropical rain forest. Morphological evidence of the tropical origin of the orange is abundant, its tropical mesophytic nature being indicated by glossy, broad, flat leaves of rather loose and open cell structure, long life of leaves, absence of stomatal devices for regulating transpiration, lack of root hairs, and lack of a regular and non-interruptable period of dormancy. Livingston[1] has recently pointed out that the most efficient climate for plant growth in the United States is peninsular or tropical Florida. The significance of this is apparent when we remember that tropical Florida is the only place in the United States where the orange has run wild and been able so to maintain itself. In all countries where the sweet orange has run wild after having been introduced into the New World, such as Brazil, Paraguay, northern Argentina, and to some extent in Florida, the climate is distinctly tropical.

Horticulturists have called attention to the fact that an environmental complex which is most efficient as regards plant growth does not necessarily conduce to the production of fruit of high commercial value. On the other hand, some climatic factors, such as light and heat,

* Manuscript submitted January 17, 1918.

[1] Physiol. Res., vol. 1, April, 1916.

which in excessive amounts tend to retard vegetative growth, intensify certain characteristics of the fruit which greatly enhance its market value. Thus we find that the Bahia or Washington Navel variety of *Citrus sinensis* has comparatively little commercial value at Bahia, Brazil, where it originated, or in any other tropical country where it has been tested. In a semitropical desert environment, however, this variety of orange is high in sugar content, has skin characteristics which lessen decay in transit, and is possessed of a deep reddish orange color which increases its salability. For these reasons the cultivation of oranges under arid and semiarid conditions has developed into an industry of large importance, in which many millions of dollars are invested and upon which many thousands of people are dependent for a livelihood.

When we consider the morphological characteristics of the more or less xerophytic vegetation indigenous to the region now occupied by orange orchards in California and note the striking dissimilarity between the forms of native plants and citrus trees, we may reasonably suspect that our orange trees may find it more or less difficult to adjust themselves to the new and strange environment. Perhaps the underground environment provided by soils which, on account of low rainfall and consequent lack of leaching, still retain a large proportion of the soluble salts resulting from the decomposition of soil minerals, would be equally as disordered as the above-ground environment were it not for the fact that water artificially applied by irrigation lessens the asperity of the conditions met by the roots. Not only is the total environmental complex to which our orange trees are exposed inconsistent with their natural requirements, but the trees of the Washington Navel variety are themselves decidedly abnormal. It is the universal practice to place scions of the desired variety upon rootstocks of other species of *Citrus* so that the reciprocal influences between stock and scion come into full play. Moreover, the variety in question bears some indications of hybrid origin. The blossoms are entirely devoid of viable pollen, functional ovules are few, the fruits are partially double, peculiar in structure and seedless, and the vegetative parts exhibit an erratic polymorphism which has so far proved decidedly puzzling.

It is a matter of common observation that in the interior desert-like valleys of the arid southwest the Navel orange is somewhat dwarfed in stature, the leaves tend to persist to an unusual age, the volume of bloom is abnormally large, shedding of the flowers and young fruits is

excessive, and various physiological derangements of nutrition are of frequent occurrence.

In many interior localities where there are but few pests to hinder the growth of the tree and where the climatic conditions favor the production of early maturing fruit of good color and high sugar content, the excessive shedding of young fruits, or "June drop," as it is called, is particularly exasperating to growers, who would undoubtedly make much greater profits if some way could be devised to prevent that part of the drop which is in excess of the normal and necessary amount. An investigation of this problem was undertaken by the writers in response to a resolution passed by the California State Fruit Growers' Convention calling the attention of the university authorities to the urgent need of an investigation of this subject. The results secured from observations and experiments during the summers of 1916 and 1917 are brought together in his paper.

Most of the field experiments from which our data have been obtained were carried on at two stations in Kern County; one at Edison in the orchards of the Edison Land and Water Company, about eight miles southeast of Bakersfield, and the other about two miles and a half distant at East Bakersfield in the orchard of Dr. C. W. Kellogg. Both stations, on account of being situated to leeward of a considerable stretch of desert typical of the southern San Joaquin Valley, experience the extreme climatic conditions referred to above. The Navel orange matures early and is of excellent quality, and were it not for the light crops borne this district would be considered excellent for the production of Navel oranges. Under these climatic conditions, unmodified, the drop occurs every year and is not dependent on the occurrence of dry hot winds, as is the case in southern California.

At Edison the Navel orange trees appear healthy and vigorous, the leaves and branches being quite free from fungous parasites and scale insects. Except for an occasional slight showing of mottled-leaf disease the trees may be considered very thrifty and of good size for their age, which is eight years. A general view in this orchard is shown in plate 25.

The soil conditions are good. The type is Delano sandy loam of good depth. No general layer of hardpan exists. Although certain bodies of hard conglomerate occur occasionally these are not in layer formation and do not interfere with the drainage. The soil is rich in most plant foods, though low in nitrogn, which, according to an analysis kindly made by Dr. C. B. Lipman, runs from .025 per cent in

the first six inches to .012 per cent at a depth of three feet. He also reports the nitrifying power of the soil as fairly good and the ammonifying power as high. The organic matter content is quite low, much lower, in fact, than one would suppose from the healthy appearance of the trees.

Irrigation water is pumped from wells situated on the tract and the irrigation practice follows closely that of southern California. Water is applied in four shallow furrows to each middle about once a month. This is followed in a few days by shallow cultivation in both directions. The amount of water applied is sufficient to wet the soil five feet deep and throughout the whole area except for a small space between the trees in each tree row. In June the temperature of the water as used is about 75° F. Hilgard advanced the idea that June drop might be caused by low temperature of the irrigation water. While it is entirely possible that cold water may influence drop, we have found the drop to occur regularly where the water was not cold.

TABLE 1

MOISTURE DETERMINATIONS IN EDISON SOIL
Furrows run north and south

Location of sample with reference to tree	Depth	Per cent moisture based on water-free soil: Before irrigating	After irrigating
North side	6 in.	5.70	6.38
North side	20 in.	5.04	6.95
East side	6 in.	6.72	12.61
East side	20 in.	7.99	10.25
South side	6 in.	5.70	6.04
South side	20 in.	7.87	7.29
West side	6 in.	7.52	11.48
West side	20 in.	7.06	11.60

A practical horticulturist after examining the trees and digging into the soil would hardly conclude that the trees were suffering for water. Moreover, Fortier states[2] that in sandy loam soils 6 per cent by weight of free water is sufficient to keep citrus trees in a vigorous condition. In the Riverside-Redlands districts the average moisture content of the soils in citrus orchards runs from 4 to 9 per cent, depending on the soil type. In spite of this it is possible, of course, that the average moisture content of the Edison soil is below the optimum.

The management of the orchard consists of clean shallow cultivation throughout the year with a fairly deep plowing in March. No cover crops have as yet been grown. Light applications of manure and com-

[2] Irrigation of Orchards, U. S. Dept. Agr. Farmers' Bull. no. 404 (1910) p. 24.

mercial fertilizers are given. The roots of the trees fully occupy all of the middle spaces, and appear exceptionally healthy and vigorous. A large number of healthy roots were taken from a hole dug at the center of a square formed by four trees. The vertical distribution of roots is good. A hole two feet square was dug to the southwest of a tree well beyond the spread of the branches. Each six-inch soil layer was kept separate and the roots sifted out. On account of the dryness of the air comparative weights were not made, but the root distribution between the second and sixth six-inch layer is well shown in plate 42.

The general health and appearance of the trees at the Kellogg orchard is in every way similar to that at Edison. The orchard is one year younger than the plot used in the experimental work at Edison, but there is no appreciable difference in the size of the trees, unless it be in favor of the trees at the Kellogg place, which is to be explained as due to the method of handling the orchard.

Soil conditions are fairly similar, except that the surface soil at Edison is considerably heavier and more compact than at East Bakersfield, where the soil would be classified as a medium sand. However, it becomes heavier as one goes down until, at a depth of two feet, there is no noticeable difference in the soil at the two stations. We are not able to present analyses of this soil as to plant food, but there is no reason to believe that it differs markedly from that at Edison.

A radical difference, however, is manifest in the management of the two orchards. The main part of the Kellogg orchard is planted to alfalfa (pl. 26), and the portions in which our experimental work was done have had alfalfa grown between the trees for three or four years. Before planting the alfalfa the orchard was carefully and effectively laid out in small checks draining one into the other. The trees are protected from having water standing about their trunks by ridges thrown up just under the drip of the trees. These checks as well as the ridges are occupied by a good stand of alfalfa, which is cut for hay and hauled off. Irrigation water is pumped from wells and is applied in copious amounts, the period between irrigations averaging about three weeks, or a week to ten days shorter than that at Edison. There can hardly be any doubt but that considerably more water is applied to these trees than at Edison. Applications of commercial fertilizers have been made to the orchard from time to time. No detailed study of the root distribution was made but a few holes dug for other purposes seemed to indicate that the roots tend to go down or away from the surface in this orchard rather than to be localized in the upper soil layers.

Another distinctive feature of the Kellogg orchard is that it is protected on three sides by a fairly efficient windbreak. On the north, from which direction the prevailing winds blow, this consists of a double row of pepper trees (*Schinus molle*), and a single row of poplars. On the other two protected sides, the east and the west, there are rows of eucalyptus.

The Nature of June Drop

A cursory investigation of the problem at once established the fact that the young oranges are shed while still alive and actively functioning and as such the shedding constitutes true abscission. It is of course quite a different process from exfoliation, which involves the formation and activity of a phellogen. Before proceeding to a discussion of the process of abscission as determined by us, it may be well to discuss the amount of bloom, time of abscission, reaction time, and other important features.

Navel orange trees growing under the conditions studied always bloom very heavily (pls. 27, 28, and 29). The blossoms are borne on shoots of the current season's growth, being preceded and accompanied by new leaves. The old leaves do not fall until anthesis is well under way or completed. It is evident, therefore, that during anthesis the trees are under a heavy drain, inasmuch as they are called upon to support a heavy bloom in addition to both the new and old crops of leaves. Shedding of the unopened flower buds occurs to a small extent only. The opened flowers exhibit a certain amount of dimorphism. Those capable of setting fruit possess large, fully formed ovaries, with plump styles and stigmas. In many of the flowers, however, the pistils show a varying degree of degeneration and shedding of the flowers is largely confined to such individuals, beginning with the least robust and grading off during petal fall and including many of the most robust after petal fall. The period of maximum shedding takes place when the young fruits are from one-half to two centimeters in diameter. At first the point of abscission is always at the base of the pedicel (pl. 30), but after the diameter of the fruit has reached one centimeter or thereabouts it is usually at the base of the ovary. It is interesting to note that where the larger fruits absciss at the base of the ovary, abscission usually occurs also in the cortex at the base of the pedicel; but on account of the formation of strengthening tissue the process is not completed through the vascular elements and although the pedicel dies, it remains very firmly attached to the twig. This is shown in plate 31. It often happens that a certain amount of strength-

ening tissue at the base of the ovary may prevent the fall of the fruit. These dead, dry fruits, as shown in plate 31, are often quite conspicuous on the trees. Soon after the application of the stimulus, but several days before actual separation, the larger fruits assume a characteristic appearance, losing their luster and taking on a lighter green color. In the case of exposed fruits the yellow color is deeper around the apex, but this is not the case with shaded fruits. It is thus a simple matter to select any number of fruits which are destined to absciss several days before separation actually occurs.

Experiments carried on in the laboratory and observations made in the field, both in a survey of the citrus districts of southern California immediately following the heat wave of June 15–17, 1917, and at Bakersfield during 1916 and 1917, have shown that the time intervening between the application of the stimulus and actual separation is from four to ten days. The shorter periods were obtained in the laboratory, where the room temperature was uniformly high. Our observations are that under field conditions abscission is ordinarily complete within five to eight days after the application of the stimulus.

Normally, orange blossoms, being borne in cymes, open in succession, beginning about March 20 in the San Joaquin Valley and continuing about one month. Abscission varies with the season but usually it is in evidence from April 1 to about July 1, a period of three months. The period of maximum shedding occurs during the latter half of April. It should be noted that the season of 1917 was unique in being the latest on record. Protracted cool weather delayed the bloom fully five weeks, with a consequent delay of the period of maximum shedding. A comparison of the mean maximum atmospheric temperatures for the years 1914–17 inclusive is shown in table 2. The comparative lateness of the 1917 season is apparent from a study of this table.

TABLE 2

MONTHLY MEAN MAXIMUM TEMPERATURES FOR TEN MONTHS AT BAKERSFIELD

Compiled from U. S. Weather Bureau Records

	1914	1915	1916	1917
January	61.2	60.3	57.8	59.3
February	67.9	65.2	69.9	68.2
March	75.8	71.8	73.8	69.5
April	78.5	75.3	81.6	74.7
May	86.6	77.5	81.1	77.4
June	94.7	92.8	93.0	95.6
July	100.2	98.8	99.0	104.4
August	101.9	101.5	95.2	100.5
September	88.0	91.9	93.2	94.3
October	82.9	87.8	76.1	88.5

Turning now to a more detailed account of the abscission process itself we find that this subject has received considerable study and investigation. The nature of the abscission process has been studied and described in detail by Hannig[3] and Lloyd[4] for *Mirabilis;* Balls[5] and Lloyd[6] for *Gossypium;* Loewi[7] for *Ampelopsis;* Kubart[8] for *Syringa* and *Nicotiana;* Kendall[9] for *Nicotiana;* Tison[10] and Lee[11] for many other plants, to mention only a few of the researches in this interesting field. While the histology of abscission in *Citrus* has been described in detail elsewhere[12] by the junior author, it is appropriate that a brief sketch be included here.

As previously indicated, there are two entirely distinct abscission zones. One is at the base of the pedicel and the other at the base of the ovary. In each case the zone may be considered to be situated at the base of an internode where, on account of the power of forming adventitious buds, it may reasonably be suspected that the tissue retains, to a degree at least, its meristematic nature. The zones consist of ten to eighteen layers of cells which in young tissue differ histologically very little, if any, from adjacent tissues. In older material differences involving shape, size, and content appear. That in the case of young tissue differences of some kind do exist is shown by the fact that after the stimulus has been applied, yet ten to fifteen hours before visible indications appear, the walls of abscission cells are differentiated by a marked inability to hold certain stains, such as methylen blue. From six to eight hours before abscission the walls of the abscission cells are refractive to a different degree.

The first indication of actual abscission is a marked swelling and and gelatinization of the walls, which may amount to as much as 200

[3] Untersuchungen über das Abstossen von Blüten, Zeitschr. f. Bot., vol. 5 (1913), p. 417.

[4] Abscission in *Mirabilis Jalapa*, Bot. Gaz., vol 61 (1916), pp. 213–30, pl. 13.

[5] The Cotton Plant in Egypt (London, Macmillan, 1912), p. 69.

[6] The Abscission of Flower-buds and Fruits in Gossypium, and its Relation to Environmental Changes, Trans. Roy. Soc. Canada, ser. 3, vol. 10 (1916), pp. 55–61.

[7] Blättablösung und verwandte Erscheinungen, Vienna Acad. Proc., vol. 1 (1907), pp. 166–983; S-B. d. math.-nat. Kl. d. k. Akad. Wiss., Wien, vol. 116, abt. 1 (1907), pp. 983–1024.

[8] Die organische Ablösuug der Korollen nebst Bemerkungen über die mohlsche Trennungsschicht, *Ibid.*, vol. 115 (1906), p. 1491.

[9] Abscission of Flowers and Fruits in the Solonaceae with special reference to *Nicotiana*, Univ. Calif. Publ. Bot., vol. 5 (1918), pp. 347–428.

[10] Recherches sur la chute des feuilles chez les Dicotylédones, Mém. Soc. Linn. Normandie, vol. 20 (1900), p. 125.

[11] The Morphology of Leaf Fall, Ann. Bot., vol. 25 (1911), pp. 51–106.

[12] An Account of the Mode of Foliar Abscission in *Citrus*, Univ. Calif. Publ. Bot., vol. 6 (1918), pp. 417–28.

to 300 per cent. This is followed by dissolution of the gelatinous walls, thus freeing the cells which are now surrounded merely by the very thin and delicate tertiary membrane. No elongation of the tertiary membrane has been observed. Neither has any cell division prior to separation been seen to occur, although immediately following separation this often takes place. So far as ascertained, therefore, abscission in the orange conforms to the usual type, e.g., schizolysis[13] representing dissolution of the middle lamellae of the abscission zone cells by hydrolysis with subsequent separation.

Stimuli Leading to Abscission

The direct cause of abscission in plants in general is considered to be some stimulus which may be brought into play in a variety of ways, depending somewhat on the nature of the plant involved. Lloyd[14] has taken pains to enumerate some of the different kinds of stimuli which according to various writers have been found to cause abscission. It is our purpose to consider these in turn as a possible cause of abscission in the Navel orange and possibly by elimination to arrive at the true cause or causes involved.

Mechanical Shock or Traumatic Stimuli

Fitting[15] has shown that jarring or shaking the flower stalks of *Verbascum* sp. and *Geranium pyrenaicum* will result in abscission within a few minutes. We were unable to produce like results with *Citrus* by this method. Moreover, abscission has been observed to occur regularly under conditions which would preclude the possibility of this cause being operative with oranges.

An effort was made to cause abscission by cutting and bruising the young fruits in various ways. The result was a failure in every case. Excision of the style and petals either separately or together, either before or during anthesis, failed to produce abscission. Many of the fruits from which the style had been removed developed to maturity in a normal way. Others abscissed but the reaction time varied so widely as to make it very improbable that the removal of the style was the stimulus involved.

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13 Correns, Vermehrung der Laubmoose, Jena, 1899. (Cited from Lloyd.)

14 Abscission, Ottawa Naturalist, vol. 28 (1914), pp. 41–52, 61–75.

15 Untersuchungen über die vorzeitige Entblätterung von Blüten, Jahrb., f. Wiss. Bot., vol. 49 (1911), p. 187.

In many plants insect injuries have been shown to be the cause of abscission. The case of the cotton boll weevil is perhaps the best known example, though it is likely that young fruits of the plum and apple react to injuries due to the curculio[16] and codling moth[17] in much the same way. In view of these observations it is interesting to find that oranges are a marked exception to the rule, the young fruits being particularly resistant to the effects of insect wounds.[18] In the San Joaquin Valley there are two insects at least which cause serious injury to the fruit. The work of *Scirtothrips citri* results in an extensive though superficial scarring of the fruit, yet the fruit develops to maturity. The nymphs of the fork-tailed katydid, *Scudderia furcata*, eat holes in the young fruits (see pl. 32), the holes sometimes extending entirely through the orange. This insect produces traumatic stimuli of the first magnitude, yet they do not result in abscission. Large numbers of the chewed, deeply scarred and distorted fruits develop to maturity only to be discarded by the pickers at harvest time.

Mechanical shock produced by transplanting trees or the root pruning incident to heavy spring plowing, such as is necessary to turn under a rank-growing cover crop, is usually followed by more or less dropping of the leaves and fruit. It is believed, however, that this may be accounted for by the disturbance of the water relations which follows root pruning rather than by the mechanical shock alone. Balls,[19] by root pruning cotton plants in Egypt, was able to cause abscission of the bolls, which he explained on the ground of water relations rather than shock. This particular phase of the problem will be again referred to later.

Air Temperatures and Light Changes

Abnormally high air temperatures or sudden changes in the temperature are by some investigators considered the cause of abscission in certain cases. It is evident that the question of the influence of air temperature is so involved with other important questions, such as the influence of humidity, air movement, transpiring power and the like, that it is inadvisable to assign specific influences to this factor alone. The same is true of changes in light intensity. Suffice it to say, how-

[16] The Plum Curculio, U. S. Dept. Agr. Bur. Ent., Circ. 73 (1906), p. 4.

[17] The Codling Moth, *ibid.*, Yearbook (1887), p. 90.

[18] True in California, though Hubbard mentions the punctures of two insects, *Dysdercus suturellus* and *Leptoglossus phyllopus*, as causing the dropping of mature oranges in Florida. Hubbard, H. S., Insects Affecting the Orange, U. S. Dept. Agr., Div. Ent. (1885), pp. 167–69.

[19] *Loc. cit.*, p. 68.

ever, that while a sudden rise in temperature may be and often is accompanied by increased shedding rates, it has been observed by the writers that profuse shedding of the young Navel oranges takes place during periods when no sudden changes or abnormally high temperatures occur. It has also been noted that abscission of the interior and well shaded fruits takes place simultaneously with that of fully exposed fruits. It is altogether unlikely, therefore, that the June drop can be explained on these grounds alone. The relation between abscission and tissue temperatures as affected by water deficits will be discussed in another place.

Many investigators have noted the marked effect of increase in air temperatures on the time involved in the separation process, and we have noted the same phenomenon. The effect of course, as would be expected, is an acceleration conditioned by the magnitude of the temperature change. It appears therefore to the writers that abscission following sudden increases in temperature, as noted by several investigators, may be easily explained on the ground that the stimulus to abscission had been activated at some time prior to the sudden change in temperature, and the acceleration of the abscission process, producing marked results in a comparatively short period, has led them to believe that the change in temperature is the causative stimulus.

Lack of Pollination and Fertilization

While there is a general rule that pollination and fertilization is essential to the setting and development of fruits, the rule is conspicuous for its exceptions. A number of our commercially important fruits, such as bananas, Sultanina grapes, Japanese persimmons, and Navel oranges, are distinctly parthenocarpic and do not require the stimulus of pollination to insure the setting of fruits which are usually seedless. The Navel orange does not produce viable pollen, and pollen from other varieties will only occasionally accomplish fertilization for the reason that nearly all of the embryo sacs disintegrate instead of developing into normal ovules capable of being fertilized.[20] Occasionally a few normal embryo sacs may be produced and seeds result provided the particular fruits having the normal embryo sacs happen to be pollinated with viable pollen from congenial varieties. It is the remoteness of the chance of this occurring under ordinary field conditions that accounts for the comparative seedlessness of these fruits. Apparently there is nothing in the structure of the blossom of the

[20] Ikeda, T., On the Parthenocarpy of Citrus Fruits, Jour. Sci. Agr. Soc. Tokyo, vol. 63 (1904).

Navel orange which would interfere with the germination of pollen or the normal extension of the pollen tube. The exclusion of pollen by the bagging method has shown that in setting fruit the Navel orange is entirely independent of pollen. This experimental evidence is borne out by the practical experience of growers who secure as abundant crops from large isolated plantings of Navels as from mixed plantings. It is therefore entirely safe to conclude that lack of pollination and fertilization of the Navel orange does not result in the stimulus leading to abscission.

Relative Position on Stem

There is some variation in the relation borne by orange fruits to the main supporting axis. As it has been suggested that with some other plants this relation largely determines whether a given fruit will be able to persist, it was thought worth while to investigate the importance of this point in connection with oranges. A large number of fruits were examined and divided into two classes: those which terminated the axis, and those which did not. These two classes are well illustrated in plate 33. It seems reasonable to suppose that in the case of the non-terminals, an organ of limited secondary thickening (the pedicel) being in competition with one of unlimited secondary thickening (the main axis) might suffer from an increasing prejudice to its water supply. It was found by counts of large numbers of fruits that the ratio of terminals to non-terminals was 5 to 6. The new current season's growth which bore terminal fruits averaged 3.8 leaves per shoot, while the non-terminals averaged 3.95 leaves per shoot. In the latter case 1.85 leaves were below and 2.1 leaves above the fruits. Counts of fruits which had successfully survived the abscission period showed on one tree 16 terminals to 31 non-terminals, but on another tree 25 terminals to 14 non-terminals. Counts of dropped fruits also failed to support the above supposition, and it is evident from our examination of large numbers of specimens that abscission in this case is quite independent of such differences in the relation of fruit to axis as is shown in plate 33.

The Gas Factor

It has long been recognized that the subjection of certain plants to an atmosphere containing traces of various narcotic or poisonous gases is sufficient to cause abscission of leaves and other plant parts. One of the first indications of smelter fume injury is the shedding of the leaves of certain plants due to the presence of sulfur dioxide, which is

a combustion product in the reduction of sulfur-containing ores. G. J. Pierce[21] has shown that when SO_2 is present in as small quantities as three to five parts per million abscission of the leaves of certain forest plants occurs. Several investigators have reported abscission of flowers and leaves of various plants when subjected to minute traces of illuminating gas, ether, chloroform, ethylene, and other poisonous gases. Further, two investigators have reported[22, 23] abscission of the leaves of citrus plants when subjected to an atmosphere containing traces of illuminating gas. We have obtained similar results with potted plants. Within four days after subjection to illuminating gas all the leaves were shed.

The exhaustive work of L. I. Knight and W. Crocker[24, 25] on the effects of illuminating gas and smoke upon plants has shown rather conclusively that the response is largely if not entirely due to the toxicity of the ethylene present. It has been shown by E. M. Harvey[26] that as minute traces as one part per million are sufficient to cause marked reactions on the part of the plant.

Preliminary experiments carried out in our laboratories with excised citrus shoots subjected to various gases, including illuminating gas, have indicated that under such conditions abscission is not appreciably accelerated by any of the gases. The time at which shedding of the leaves took place was approximately the same in ordinary room atmosphere as in varying concentrations of illuminating gas.

Peirce[27] has shown that one of the effects of smelter fumes is to cause excessive transpiration from certain plant parts prior to their abscission. This is accounted for by the decomposition of the chlorophyll in the guard cells of the stomata, resulting in decreased stomatal regulation of transpiration. As will be pointed out later, several investigators have concluded that abnormal water loss during a part of the day, resulting in considerable fluctuations in the leaf

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[21] 1. A Report of an Investigation conduteed for U. S. Department of Justice, 1913, unpublished manuscripts in the hands of U. S. Attorney General. 2. Report of Selby Commission, to U. S. Bureau of Mines, 1913.

[22] In *Citrus limonia.* Shonnard, F., The Effect of Illuminating Gas on Trees, Yonkers, N. Y., Dept. Pub. Works (1903), p. 48.

[23] In *Citrus decumana.* Doubt, Sarah S., The Response of Plants to Illuminating Gas, Bot. Gaz., vol. 63 (1917), pp. 207–24.

[24] The Effect of Illuminating Gas and Ethylene upon Flowering Carnations, Bot. Gaz., vol. 46 (1908), pp. 259–76.

[25] Toxicity of Smoke, *ibid.*, vol. 55 (1913), pp. 337–69.

[26] Some Effects of Ethylene on Metabolism of Plants, *ibid.*, vol. 60 (1915), pp. 193–214.

[27] Expert testimony incorporated in Records of Federal Court, District of Utah, Salt Lake City.

water content, is sufficient in certain plants to cause abscission. In the light of these observations abscission of plant parts when exposed to smelter fumes is explainable purely on the basis of abnormal water relations.

In an effort to ascertain whether in the case of illuminating gas any such relation holds true, we have made a careful study of the stomata of citrus leaves and have to report that at an early period in the life of the leaf they lose their power of functioning and remain practically closed thereafter. This is significant in view of our findings mentioned above, namely, that illuminating gas is not a direct stimulus to abscission in *Citrus*, at least with excised shoots. In the case of potted plants it seems probable that it works in an indirect manner through disturbances in the physiological balance. In connection with the question of the effect of illuminating gas upon the chlorophyll of the guard cells, it should be mentioned that H. M. Richards and D. T. MacDougal[28] have reported that chlorphyll formation is greatly retarded when the plant is subjected to an atmosphere containing traces of this gas.

The fumigation of citrus trees with hydrocyanic acid gas for the control of scale insects is practiced quite generally and with marked success in California. It is the general experience that under certain conditions heavy dosages of this gas result in abscission of the older leaves.[29] Researches by Osterhout[30] and Moore and Willaman[31] have shown that when subjected to traces of this gas the permeability of cytoplasmic septa is markedly altered, causing an increased loss of water. In the light of these observations it is entirely possible to explain dropping of citrus leaves due to fumigation on a purely water relation basis.

Fumigation injury to the blossoms or fruit, whether large or very small, consists of pitting and burning which results in scars on the fruit. Apparently in no case does fumigation of young Navel oranges with hydrocyanic acid gas furnish a stimulus to abscission.

The whole subject of the effect of gases in causing abscission of plant parts is in a very unsatisfactory state at the present time. In view of the mass of conflicting data, as well as the fact that abscission

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[28] The Influence of Carbon Monoxide and other Gases upon Plants, Bull. Torr. Bot. Club, vol. 31 (1904), pp. 57–66.

[29] Woodworth, C. W., and others, School of Fumigation, Pomona, California, pp. 162–64, August, 1915.

[30] Similarity in the Effects of Potassium Cyanide and of Ether, Bot. Gaz., vol. 63 (1917), pp. 77–80.

[31] Studies in Greenhouse Fumigation with Hydrocyanic Acid: Physiological Effects on the Plant, Jour. Agr. Res., vol. 11 (1917), pp. 319–38.

of young Navel oranges occurs throughout the great interior valleys of California and in districts very remote from any possible source of noxious vapors, there is little possibility that the gas factor can be operative in the case under consideration.

Fungi and Bacteria as a Cause of Abscission

Although the belief is commonly held by plant pathologists that fungus parasites sometimes cause the shedding of plant parts, the literature on this phase of abscission is very meager. Inoculations with *Bacterium citrarefaciens*, the organism causing Citrus Blast, carried on in our greenhouses have shown that when the organism is inoculated into the tip of the young leaf the latter is shed within a few days. Rolfs has reported that shedding of mature oranges frequently occurs in Florida, due to the common wither tip fungus, *Colletotrichum gleosporioides*. However, we are concerned here with the shedding of immature fruits and it is by no means clear that the process resulting in shedding is the same in both cases.

For many years growers of Washington Navel oranges have experienced losses from a black rot disease of the fruit which manifests itself as a stimulation of the fruit, causing it to grow to an extra large size, ripen early and assume a deep red color, with a certain amount of dropping. This disease was first noted by N. B. Pierce[32] in 1892 and was first described by him in 1902[33] as "Black Rot of the Navel Orange" caused by the fungus *Alternaria citri*.

The fruit is infected when quite small, probably just before or soon after the style is shed, through the cracks and imperfections in the proliferations of the navel (pl. 34). The fungus is a weak parasite and remains quiescent, or nearly so, during the growing period of the young fruit, at which time the fruit is more or less resistant to the encroachments of parasites. With the decline in vigor incident to approaching maturity the fungus becomes more active and exerts a stimulating influence on the fruit, causing it to take on a deep reddish-yellow color and to ripen earlier than the normal fruit. In a small and restricted area the cells of the pulp are broken down and become a nauseating mass of black fungus mycelia and spores. The rind is left uninjured until the disease has made considerable progress within, but ultimately a black and decayed spot appears on the surface near the navel end. A certain proportion of the infected fruits early shows a yellow spot

32 U. S. Dept. Agr. Yearbook (1892), p. 239.

33 Bot. Gaz., vol. 33 (1902), pp. 234–35.

about the navel end and drops from the tree when about one to two inches in diameter, or even larger. The remainder persist to maturity, the disease coming into evidence at picking time, in transit, in storage, or not until in the hands of the consumer.

Early in 1916 our attention was directed to the fact that on dissection a relatively large number of the shed fruits and fruits about to drop were found to have a discolored area under the navel end. In many cases a dark colored, gummy mass was present, although in others the tissue immediately under the navel was only slightly discolored (pl. 35). In some fruits there was no evidence of any such spot or area. A few of the dropped fruits were sterilized in mercuric chloride (1–1000) and placed in small moist chambers. To our surprise these cultures showed practically 100 per cent infection with an *Alternaria*. Other cultures were made with the same results. Therefore we concluded that it was well within the realm of possibility that the June drop was due to the same fungus causing black rot and decided to investigate the matter more thoroughly.

The fruits had reached a size of one or two centimeters and the blooming period was entirely over, precluding any investigation as to the source and manner of infection in 1916. Therefore our efforts in this direction during 1916 were confined to attempts to determine, if possible, the extent of the infection. Cultures of many hundreds of shed fruits, and fruits about to fall, from many districts of the state were made both by the method above described and by inserting a piece of tissue from the discolored area into slanted tubes of Shear's corn meal agar. The cultures uniformly showed a high percentage of infection with *Alternaria*. A few cultures were then made using healthy green fruits picked from the trees. The percentage of infection was small. Still later in the season dropped fruits from four to five centimeters in diameter (pl. 35) were collected from districts as far apart as Oroville in the Sacramento Valley and El Cajon near San Diego. Cultures made from these fruits showed practically 100 per cent infection.

Although the number of cultures made was too small to justify a broad generalization, the work done in 1916 was sufficiently productive to form the basis for a working hypothesis which was advanced as a theory to account for the June drop of Washington Navel oranges. Other experimental work under way had indicated the presence of certain abnormal water relations between the young fruits and the leaves immediately behind them, which phenomenon

will be discussed more fully in a later section. Briefly, the theory advanced was that excessive transpiration from the leaves caused water together with enzymatic solutions secreted by the fungus in the navel end to be drawn back through the vascular system of the young fruits through the pedicel and thus provide the stimulus to abscission.[34]

That there is no mechanical difficulty involved in this theory was borne out when by means of dyestuff solutions it was demonstrated that the vascular system running to the navel or secondary orange traverses the central pith or core of the primary fruit, which thus serves as receptacle and stem to the smaller fruit (fig. 1).

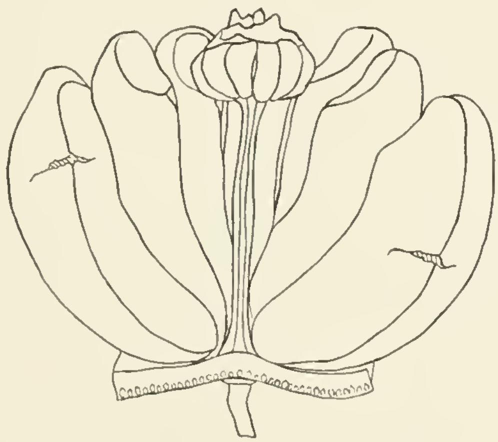

Fig. 1. Structure of the Navel orange. The central pith containing fibrovascular bundles acts as the stem of secondary fruit.

Further evidence tending to support this theory lies in the fact that black rot is much more prevalent in the interior valleys than in the coast regions. In fact, there seems to be a certain correlation between the amount of black rot and the amount of drop. The reason for the greater prevalence of black rot in the hotter, more arid districts was not uncovered until later; this will be brought out in another section.

Alternaria citri, Ellis and Pierce

During the winter of 1916 a careful study of the alternarias obtained in our cultures was made and disclosed the fact that although there were several strains of *Alternaria* obtained, one particular type rather easily recognizable after a little practice, was by far the most

[34] Coit, J. Eliot, and Hodgson, R. W., The Cause of June Drop of Washington Navel Oranges, Univ. Calif. Jour. Agr., vol. 4 (1916), p. 10.

common. In addition we obtained one strain possessing the ascigerous stage, which of course classified it in the genus *Pleospora*. Several *Macrosporium* strains were also isolated.

Considerable effort was made to identify the *Alternaria* strain so commonly found, but we have been unable to satisfy ourselves thoroughly in this regard. While the literature is indeed voluminous, there is apparently no reliable monograph of the genus. Recently, however, there has appeared a critical study of the taxonomic characters of the genus.[35] The genus *Alternaria* is one of the most universally distributed of the common forms of the *Fungi Imperfecti*. It embraces about fifty species, although it has been shown by Elliott that a large number of the species of the closely related genus *Macrosporium* really belongs to the genus *Alternaria*. Among these species we find active parasites as *A. solani* (E. and M.) J. and G., weak or facultative parasites as *A. citri* Ellis and Pierce, and saprophytes as *A. tenuis* Nees. Certain species have already been secured in the perfect or ascigerous stage which has always proved to be *Pleospora*. Since the strain under consideration was uniformly obtained from oranges in a district where black rot is common it is probably the same form found by Pierce and called *Alternaria citri*. We were unable to find the original description by him, which does not seem to have been published. However, after examining the literature and drawings of *Alternaria citri*, particularly as given by Rudolph,[36] we feel reasonably sure that we are dealing with *Alternaria citri* E. and P. and throughout the remainder of the discussion we shall proceed on that assumption.

The spores of *Alternaria citri* are borne in long chains (pl. 36), which readily break up, allowing the spores to float away in the air. It seemed important to determine whether the infection of oranges was accomplished by spores borne by the air or those carried by honeybees and other insects. The following methods were employed. Petri dishes containing Shear's corn meal agar were exposed for five minutes in different localities. After a few days had elapsed in order to allow the various bacteria, molds and other fungi to assume colony form and the *Alternaria*, if present, to produce spores, the dishes being inverted were placed under the low power of the microscope and the colonies of *Alternaria* easily distinguished and counted. On account of the length of the spore chains and certain other morphological

[35] Elliott, J. A., Taxonomic Characters of the Genera *Alternaria* and *Macrosporum*, Am. Jour. Bot., vol. 4 (1917), pp. 439–76.

[36] A New Leaf-Spot Disease of Cherries, Phytopathology, vol. 7 (1917), pp. 188–97.

characters which became familiar with practice, it was easy to distinguish between various other species of *Alternaria* which were occasionally met with.

The specialized cells lining the stylar canal of orange flowers secrete a pure white sugary mucilage which is exuded upon the stigma in a rather large drop. This material is an excellent medium for the growth and sporulation of *Alternaria,* as was determined by trial, the fungus fruiting heavily in a short time on smears kept in a moist chamber. In order to determine the amount of infection of blossoms in the orchard, the stigmas were clipped with sterile scissors on agar plates and the resulting growths examined a few days later for the characteristic spore chains. The data secured in this way are presented in tables 3 and 4. In the interior valleys 89 per cent of the stigmas were infected and in coast localities 76 per cent. It is found that the air generally throughout the state carries *Alternaria* spores in abundance. In interior localities *Alternaria* spores were taken in 78 per cent of exposures with ten centimeter agar plates; in some places near the coast in 63 per cent. It was also shown that while bees may and do carry spores from one blossom to another the number of spores in the air is sufficient to cause widespread infection without the aid of bees.

TABLE 3

NUTRIENT AGAR PLATES EXPOSED TO THE AIR, 1917

Locality	Date	*Alternaria* present	*Alternaria* not present
Whittier	May 3	18	3
Highland	May 6	10	0
Edison (under tent)	May 3	1	2
Oroville	May 14	10	2
Berkeley	May 17	0	4
Fresno	May 28	2	0
San Leandro	June 3	1	4
Fair Oaks	June 12	5	0
Edison (orchard)	June 22	1	2
Edison (desert)	June 22	3	2
Corona	June 27	3	0
Whittier	June 26	2	1
Riverside	June 29	6	3
Berkeley	Oct. 25	1	5

In this connection the question naturally arises as to why, if the infection of the stigmas near the coast is as great as 76 per cent, there is such a relatively small number of black rot oranges. The reason apparently lies in the fact that the average configuration of the navels

is more irregular, jagged and rough (pls. 34 and 37) in the interior valleys than in the coast districts, where the navel formation is much more commonly smooth or submerged and closed. This imperfect and open condition of the navels in the interior valleys, as will be brought out later, is due to the harsher environmental complex to which the fruits are subjected during the growing period. Everyone is familiar with the fact that fruits borne in exposed positions, particularly in the top of the tree, are very apt to be coarse and rough with large protruding navels, while the interior fruit is much finer in texture. The prevalence of *Alternaria* spores in the coast districts is certainly not much less than in the interior valleys, but the amount of infection is much less because of the smaller number of imperfect navels.

TABLE 4

MISCELLANEOUS CULTURES

Locality	Date	Kind of material	*Alternaria* present	*Alternaria* not present
Whittier	May 3	Navel blossoms	10	0
Whittier	May 3	Valencia blossoms	2	2
Highland	May 6	Navel blossoms	14	0
San José	May 25	Blossoms	4	1
Oroville	May 14	Olive blossoms	1	0
Oroville	May 14	Navel styles	8	0
Oroville	May 14	Bees about trees	3	1
Oroville	May 14	Lady bird (*Vedalia* sp.)	1	0
Berkeley	May 17	Dead style from greenhouse	0	1
Berkeley	May 17	Dead twig from greenhouse	0	1
Fresno	May 28	Orange blossoms	5	0
Sacramento	May 25	Orange blossoms	5	0
Fair Oaks	June 12	Orange blossoms	9	0
Edison	Apr. 24	Orange blossoms	11	1
Edison	Apr. 25	Bees about trees	3	3
Riverside	June 27	Citron styles	2	0
Edison	May 2	Navel blossoms	4	1
Edison	May 2	Valencia blossoms	4	0
Edison	May 2	Pomelo blossoms	2	0
Edison	May 2	Soil from under trees	0	2
Edison	May 2	Bees about trees	1	1
Edison	May 2	Navel blossoms from tented tree	6	0

As is shown in table 4, *Alternaria* spores are present on almost all the styles, both in coast and in interior valley districts. In order to ascertain whether infection occurred by the fungus growing down through the style into the navel end, material known to be infected with *Alternaria* was put up in paraffine, sectioned, and stained. Although the fungus was conspicuous on the stigmatic surface no traces of fungus mycelium could be found in the stylar tissues. This fact, together with the fact that infection is definitely correlated with the

configuration of the navel end, renders it reasonably certain that infection occurs some time after the style has been shed. The spores are probably blown and find lodgment in ragged open navels where they are held in the crevices till enfolded and overgrown by the rapidly developing ovary (pls. 34, 37). Inasmuch as the configuration of the navel as well as its size and degree of insertion are exceedingly variable, it is evident that only in a comparatively small and variable number of cases are the spores or mycelium so situated as to permit germination or growth. *Alternaria citri* is a weak parasite and cannot penetrate the unbroken skin of an orange. While it is not capable of producing any widespread breakdown in the tissues of immature oranges, it is able, after introduction into the fruit, to bring about a certain stimulus or irritation which, according to our theory, results in abscission of a certain proportion of the young fruits. It is certain that as the fruits grow and approach maturity the abnormal size, premature ripening, and extra deep color are the direct results of this stimulation. It is also considered highly probable that a certain proportion of the splitting or dehiscence of the carpels which is so serious in interior valleys is connected with the stimulation of these infections.

Referring again to the wide distribution and general prevalence of *Alternaria* spores in the air, it is evident that the spores may be transported in large numbers for great distances. The source of infection is by no means limited to the vicinity of orchards. The fungus grows readily as a saphrophyte on dead leaves, weeds, twigs, and other plant débris and it is entirely possible for spores to be brought in from forest areas in the mountains many miles away. Spores have been taken in the desert far from cultivated crops. In the dry air of the San Joaquin Valley the black rot oranges which fall under the trees are not immediately decomposed by *Penicillia*, *Fusaria*, and other fungi. They tend to mummify and after the *Alternaria* spreads through the interior it comes to the surface, and the spores there formed give these mummies a black color, as shown in plate 38. These mummies, together with the large number of abscissed styles from the blossoms, undoubtedly furnish a greatly increased supply of spores at the critical time in the development of the fruit.

A rot of apples occurring in Colorado[37] has been described as caused by an undetermined species of *Alternaria*. Judging from the drawings presented in plate 4 of Longyear's publication, the fungus is very similar to if not the same as that with which we are dealing. Moreover,

[37] Longyear, B. O., A New Apple Rot, Colorado Agr. Exp. Sta. Bull. 105, 1905.

there is a marked similarity between the modes of infection. According to Longyear (p. 7):

> The reason why certain varieties of the apple are particularly subject to the blackened seed cavity is found in a structural peculiarity of such varieties. Thus a longitudinal section through such an apple usually shows a very deep calyx tube, which, in many cases, extends to or meets the core, or even opens into it. In such cases the fungus has evidently reached the core through this passageway *by following the united styles and the inner wall of the calyx tube.* (Italics ours.)

Only certain varieties of apples, such as the Winesap, Ben Davis and a few others which have the structural peculiarities above mentioned, are found to be affected and in this connection Longyear's remarks on page 12 are of particular interest to us.

> Some of these varieties are among those which are reported as dropping their fruit badly in some seasons during June and July, but whether or not the fungus plays any part in this matter has not been determined.

The experimental work with *Alternaria* in 1917 for several reasons gave quite different results from those obtained during the previous season. As is shown in tables 3 and 4, cultures made from stigmas early in the season showed a high per cent of *Alternaria* infection. However, a very large series of cultures made somewhat later in the season, from the young fruits one-half to two centimeters in diameter, to our astonishment showed a very small per cent of infection. Culture after culture showed no *Alternaria* at all. Somewhat later, when the fruits were larger, cultures of the shed fruits showed a higher per cent of infection, while a few cultures made when the dropped fruits were four to five centimeters in diameter showed a high per cent of *Alternaria* infection.

Inasmuch as by far the greater part of the drop occurs while the fruits are one-half to two centimeters in diameter, at which time our cultures showed comparatively little *Alternaria* infection, it is evident that the shedding of this part of the crop can not be attributed to *Alternaria*. However, it is to be noted that, as was the case in 1916, toward the end of the period of shedding the dropped fruits showed a steady increase in the per cent of infection. Evidently, then, the shedding may be divided into two parts, the first including small fruits which *may or may not* be infected with *Alternaria,* the second including larger fruits which *are* infected with *Alternaria.*

Inasmuch as the climatic conditions in the San Joaquin Valley during the 1917 season were considerably more severe than in 1916

(fig. 6), and therefore the average configuration of the navels more ragged and open, to what can we attribute this difference in the amount of infection with *Alternaria?* We believe that this difference is easily explained by a study of the mean maximum temperatures for the two seasons. In table 2 these are shown for the years 1914–17 inclusive. For the 1917 season, taking the months of January and February, we see that they are about average for the last four years. March is four or five degrees below the average, April still more, and even May is below the average. June is several degrees above the average for the last four years and July shows an average mean maximum temperature of 104.4° F, considerably above the average. In other words, the early part of the season was cooler than usual and the bloom was delayed a month or more. Coincident with the end of the blooming period the weather changed radically and became very hot and dry and continued so for at least three months. Conditions were unfavorable for infection by *Alternaria;* its growth was inhibited although the spores were present. In fact, the amount of drop due to *Alternaria* in 1917 is practically negligible, and this is supported by the fact that there were very few black rot oranges at Edison at harvest time. On the other hand, the season of 1916 was noted as a relatively cool, pleasant summer and as such was favorable for infection by *Alternaria*, with the result that there were many black rot oranges.

In this connection the question arises, why are not other citrus varieties grown in these arid districts subject to infection by *Alternaria* with a consequent shedding and loss due to black rot? The answer apparently lies in two facts: that other varieties are not so susceptible to shedding, which will be discussed later, nor are they morphologically adapted to infection by the fungus. Plate 39 shows the apical end of a small Valencia orange highly magnified and it is evident that there is no favorable entrance for the fungus spores. Plate 34 shows a similar view of a Navel orange with very favorable conditions for the lodgment of fungus spores.

During the course of these investigations a great deal of time and effort was devoted to attempts to ascertain by inoculation methods whether the stimulus of *Alternaria citri* which manifested itself so clearly in the change of color of the fruit might not also be the cause of abscission of the young fruits. On account of several peculiar difficulties inherent in this particular problem we have so far been unable to secure conclusive results. The three most important of these difficulties may be mentioned briefly as follows:

1. Referring again to plate 29, it is apparent that the excessive number of buds occasions a severe struggle for survival, only a comparatively small number being able to acquire water and food sufficient for development. As it is impossible to determine in advance which if any of a group of similar buds is destined to remain, it is evident that if the sterile stigmas of all are inoculated just previous to opening many will eventually fall from other causes. Moreover, the considerable period of time involved and the frequent necessary opening and closing of the bags in an atmosphere shown to be filled with spores would introduce an element of serious error. Plate 40 shows one of a number of trees used futilely in efforts to get results in this way.

2. Orange flowers are dimorphic, as before mentioned, a certain number being destined to fall because the ovary is not capable of development. The configuration of the navel is to a certain extent fortuitous. In some cases the epidermal folds are so adjusted as to admit infection, in others not. It is obviously out of the question to examine each fruit frequently and with sufficient minuteness to determine whether during growth an opening sufficient for the entrance of the fungus was or was not available.

3. A species of aphis is very common on *Malva* and other weeds under the trees. For some reason not at present clear, the insect is unable to increase to any extent when feeding on the orange leaves in the open. However, it was found that whenever a twig was enclosed in a paper bag or a tree enclosed in a cheesecloth tent (pl. 40) the aphis multiplied at an astonishing rate. In about half the bags on the tree shown the twigs were defoliated and killed by the sudden development of a mass of aphis from young and minute individuals which were inadvertently included within the bags in spite of all precautions.

Summing up the relation between *Alternaria* and that part of the June drop with which it is always associated, we have to conclude that inasmuch as the presence of the fungus and its ability to provide a certain stimulus have been demonstrated, it is not unreasonable to suppose that abscission may be another manifestation of the same stimulus both in the case of Navel oranges and in the apple varieties referred to above. Satisfactory scientific evidence of this point, however, is lacking as yet.

The Relation of Abscission to the Environmental Complex

It has long been noted that there exists a marked correlation between climatic conditions and the prevalence and amount of the June drop. This correlation has been discussed somewhat by the junior author in another place[38] and has been reflected in the general attitude of growers who are prone to assign June drop to hot north winds, sudden changes in temperature, and other causes, most of which are climatic in nature.

In order to obtain more accurate information in this regard an investigation of the yield per tree in different citrus districts, where all other factors except the climatic complex were comparable, was carried out during the season of 1917. The results were striking and show most pronounced correlation between climatic conditions and yield when all other factors such as orchard management, etc., are fairly comparable. It was found that, assigning a yield of 100 per cent to the district averaging the highest crop, which district is characterized by considerable summer heat but moderate atmospheric humidity, the farther inland the district lies the smaller is the crop. This is precisely the order in which the asperity of the environmental complex is heightened, the atmospheric humidity decreasing and the average summer temperature increasing. Moreover, and more important, distance from the coast brings with it increasing liability to sudden changes in the weather which react most unfavorably on crops, particularly when in certain stages. The districts where these climatic conditions are most severe, namely, the Coachella Valley and the southern San Joaquin Valley, show a yield of approximately 25 per cent of that of the most climatically favored district. At intermediate stations the extent of the drop and consequently the size of the crop is easily correlated with weather conditions during the critical period. This was exemplified by the almost total loss of the Navel crop in the district between Corona and Redlands in 1917, when a dry north wind of unprecedented severity was accompanied by maximum daily temperatures as high as 118°–120° F from June 15 to 17.

This correlation between asperity of climatic conditions and amount of crop, or what amounts to the same thing, the prevalence of dropping, was very apparent in the orchard where our experimental work was done at Edison. The yield from the particular ten-acre tract used was

[38] Hodgson, Robert W., Some Abnormal Water Relations in Citrus Trees of the Arid Southwest and their Possible Significance, Univ. Calif. Publ. Agr. Sci., vol. 3 (1917), pp. 37–54.

56 per cent less in 1917 than in 1916 though the trees were a year older and should have yielded more. The asperity of climatic conditions during the critical period in 1917 as integraded in the Livingston white porous cup atmometer (pl. 41) was approximately 40 per cent greater than during the same period in 1916. This fact is brought out in table 5, where the water loss from atmometers at different stations in the United States is shown. "Grove" station in 1916 is fairly comparable with "Cultivated" station in 1917, as is the case with the two "Desert" stations. Further evidence of this correlation is afforded by the mean maximum temperatures obtaining during the critical period in the development of the young fruit (table 2). During this period in 1917 (June and July) the mean maximum temperatures were 95°.6 F and 104°.4 F respectively, while those for the critical period in 1916 (May and June) were only 81°.1 F and 93°.0 F.

TABLE 5

Comparative Loss from Cylindrical White Porous Cup Atmometers at Different Stations in the United States for the Month of June

Station	Average daily loss for 24 hours in cc.
Miami, Fla.*	15.9
Urbana, Illinois*	16.1
"Alfalfa" Station, East Bakersfield, 1917	18.5
Whittier, Calif., 1912	22.8
Berkeley, Calif., 1917	23.1
West Raleigh, North Carolina*	28.0
Gainesville, Florida*	28.7
"Tree" Station, Edison, 1916	32.9
San Diego, Calif.*	33.0
Cameron, Louisiana*	33.4
"Tree" Station, East Bakersfield, 1917	35.8
Riverside, Calif., 1912	43.4
Dickinson, North Dakota*	45.0
"Grove" Station, Edison, 1916	48.1
"Yard" Station, Edison, 1916	55.1
"Desert" Station, Edison, 1916	69.1
Reno, Nevada*	69.5
"Cultivated" Station, East Bakersfield, 1917	71.7
Tucson, Arizona*	73.0
Dalhart, Texas*	80.7
"Desert" Station, East Bakersfield, 1917	94.0

* Livingston, B. E., A Study of the Relation between Summer Evaporation Intensity and Centers of Plant Distribution in the United States, Plant World, vol. 14 (1911), pp. 205–22.

This correlation is again reflected in the comparative yields in general throughout the state in the seasons of 1916 and 1917. The latter season has been noted for its long continued, high temperatures

and low humidity, while the former was as equally marked by its relatively low temperatures and equableness. The crop in 1917 over the entire state is not estimated to be more than 40 to 50 per cent of that in 1916.

All the more recent fundamental work in plant physiology has indicated that for plants growing in the open the water relation is the limiting factor. It is at once obvious that under the conditions obtaining in the arid southwest it is the water relation which is most likely to be strained. This is particularly to be considered in connection with the previously mentioned fact that the genus *Citrus* is undoubtedly of tropical origin and therefore not well adapted by nature to withstand the tremendous water loss incident to the severe climatic complex obtaining under arid conditions.

Evidence that abnormal water relations due to the influence of the environmental complex may furnish the stimulus to abscission is not lacking. In regard to the cotton plant Balls[39] says: "It is certain that the main factor, if not the only one, is the water-content of the plant." Lloyd,[40] also working with cotton, concludes that "the water deficit is the cause of rise of temperature in the tissues, and this constitutes the stimulus which directly leads to abscission." Howard[41] has noted the fact that abnormal water conditions in the soil are immediately shown in the indigo plant, *Indigofera arrecta*, by leaf-fall or by the shedding of flowers without setting seed. His interpretation of these results will be referred to later. The junior author has already presented data to show that at Edison an abnormal water relation does exist in orange leaves and young fruits during the critical period.[42] He has shown that a daily water deficit of 25 to 30 per cent occurs in the young fruits, which deficit is made up at night. These deficits are at their maxima during the afternoon, at which period the atmospheric pull on the plant for water is at its maximum. A contributing factor to these water deficits lies in the fact that under stress of the tremendous atmospheric pull for water the leaves actually appropriate water from the young fruits. This strain on the plant is not localized but extends throughout the tree. Tensions developed by exterior foliage are transmitted quickly to interior fruits and even to distant roots as was shown by several experiments; for the sake of brevity only one will be described.

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39 *Loc. cit.*, p. 69.

40 The Abscission of Flower-buds and Fruits in *Gossypium*, and its Relation to Environmental Changes, Trans. Roy. Soc. Canada, ser. 3, vol. 10 (1916), p. 61.

41 Soil Aeration in Agriculture, Agr. Res. Inst. Pusa, Bull. 61, 1916.

42 *Loc. cit.*

On May 4, 1916, a large number of apparently healthy terminal fruits about one-half inch in diameter were selected on six trees at Edison. Lot A was left as a check, lot B was treated by clipping off with scissors one-third of the leaves of the current season's growth behind the fruit. Lot C suffered excision of two-thirds of the leaf area, and lot D had all of the leaves removed, leaving the fruit terminating a bare stem about six inches long. Unfortunately, a few of the limbs in these trees were removed by tree pruners. On November 16 the remaining labels were located and a record made of the number of fruits which persisted to maturity.

TABLE 6

EFFECT OF REDUCTION OF ADJACENT LEAF AREA ON ABSCISSION

	Number labeled	Number labels found	Number of fruit set
A. Check, not treated	200	165	29
B. One-third leaf area removed	200	163	19
C. Two-thirds leaf area removed	200	176	37
D. All leaves removed	200	167	21

Thus we see that the reduction of adjacent leaf area had no effect on the drop and inasmuch as eosin solution was drawn through oranges *in situ* to the stem in lot D very nearly as quickly as in lot A, it is evident that the tensions referred to have to do with the tracheal system as a whole, as is to be expected, and do not tend to be localized in any particular part of the tree.

TABLE 7

PRESENCE OF LITHIUM NITRATE IN LEAVES BEHIND FRUITS INJECTED WITH DRY CRYSTALS AS SHOWN BY THE SPECTROSCOPE

Experiment began at 12 M.

Time	First leaf	Second leaf	Third leaf	Fourth leaf	Fifth leaf	Sixth leaf	Seventh leaf	Twelfth leaf
12:30 P.M. 30 minutes	Positive	Positive	Positive	Negative	Negative	....	Negative	....
1:00 P.M. 1 hour	Positive	....	....	....	Positive	Negative	....	....
2:00 P.M. 2 hours	Positive	....	....	Positive	....	....	....	Negative
3:00 P.M. 3 hours	Positive	....	....	Positive	....	....	....	....
4:00 P.M. 4 hours	Positive	....	....	....	Positive	Positive	....	....
12:00 M. 24 hours	Very slight trace	Very slight trace	Negative	Trace (?)	....	....	....	....
Check	Negative	Negative	....	....	....	....	....	....

The withdrawal of water from the fruits by the leaves has been further substantiated by the use of dry crystals of lithium nitrate injected into the navel end of the young fruits and testing for lithium in the leaves proximal to the fruits at different periods following injection by means of the spectroscope. These results are summarized in table 7, where it can be seen that within a half hour, in spite of the fact that the lithium nitrate was injected dry into the fruit and had to go into solution in the freed cell sap, its presence was shown in the leaves behind the fruits.

Water relations of this same general sort have been established by a number of other investigators in plants where such deficits do not constitute a stimulus to abscission. Under this category are to be classed Renner's[43] "sätigungsdefizit" and the phenomenon of "incipient drying" described by Livingston and Brown[44] and established in other plants by Lloyd[45] and Edith B. Shreve.[46]

To determine actually the ultimate connection between abnormal water relations of the type noted and the abscission of young fruits has constituted a most difficult problem, and the evidence indicating such a connection has been obtained from several different lines of attack. Although not as conclusive as could be desired, still we believe that it is sufficient to indicate in general the relation between the two. It is hoped that additional evidence can be obtained during the next season, which evidence we were unable to get during our investigation through lack of sufficient equipment and apparatus.

As was mentioned in the description of the East Bakersfield station, this orchard is planted to alfalfa, protected by an efficient windbreak, and heavily irrigated. The noteworthy fact, however, is *that this orchard habitually bears crops in every way comparable to orchards of the same age and general treatment located near the coast.* Although situated only three and one-half miles from the Edison station and having the same exposure, the trees being one year younger, and all conditions similar in every way with the exceptions noted, this orchard

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[43] Experimentelle Beiträge zur Kenntnis der Wasserbewegung, Flora, vol. 103 (1911), pp. 171–247.

[44] Relation of the daily march of transpiration to variations in the water content of foliage leaves, Bot. Gaz., vol. 53 (1912), pp. 309–30.

[45] The Relation of Transpiration and Stomatal Movement to the Water Content of the Leaves of *Fouquieria splendens*, Plant World, vol. 15 (1912), pp. 1–14; Leaf Water and Stomatal Movement in *Gossypium* and a Method of Direct Visual Observation of Stomata *in situ*, Bull. Torr. Bot. Club, vol. 40 (1913), pp. 1–26.

[46] The daily march of transpiration in a desert perennial, Carnegie Inst. Washington, Publ. 194, 1914.

bears heavy crops (pl. 26), and has been profitable ever since it came into bearing three to four years ago.

The conclusion cannot but be forced that in the exceptions noted lies the secret of the heavy set of fruits. In order to obtain some idea of the climatic conditions obtaining within this orchard as compared with those under Edison conditions we had recourse to what metero-

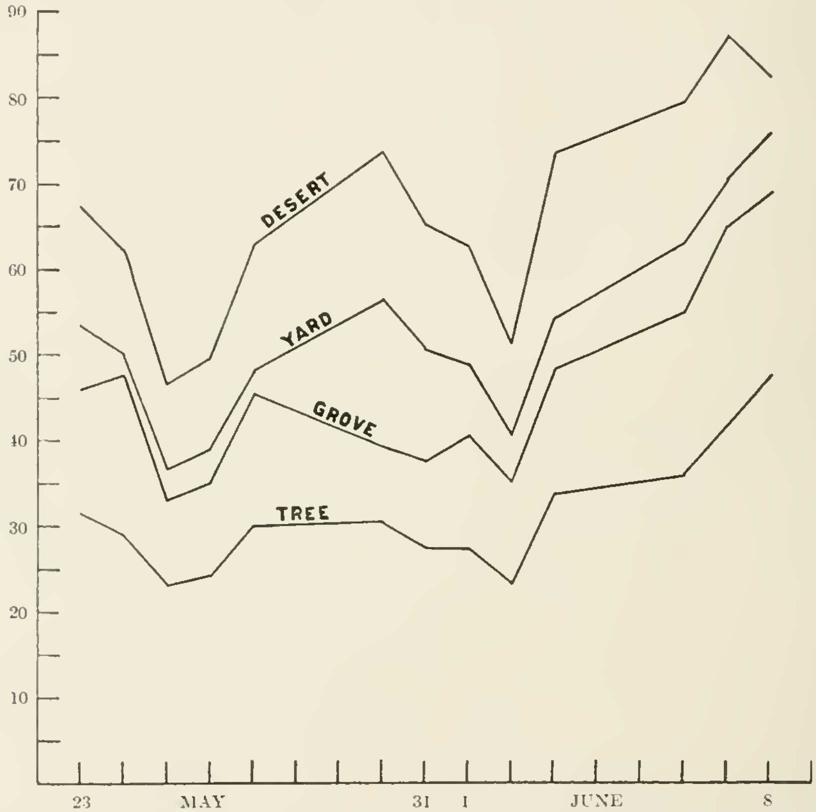

Fig. 2. Comparison of daily atmometer water loss at four different stations at Edison in 1916. Ordinates, water loss in cc.; abscissae, days of the month.

logical instruments were available to us. While much more significant results could have been obtained had we possessed more equipment, we feel that our data, while possibly not accurately quantitative, at least are qualitative enough to justify our conclusions. Air temperature and humidity readings were taken by means of a Freiz thermo-hygrograph. We were particularly interested, however, in the integration of all the climatic factors in their effect upon the plant and for this purpose selected the Livingston white cylindrical porous cup atmo-

meter[47] (pl. 41). We are cognizant of criticisms of this instrument by Briggs and Shantz,[48] but believe that for our purpose it is sufficiently accurate. Due to a lack of a sufficient number of these instruments we were unable to run a series simultaneously at Edison and at East Bakersfield but we did operate them under as nearly similar conditions at the latter place in 1917 as at the former in 1916. Know-

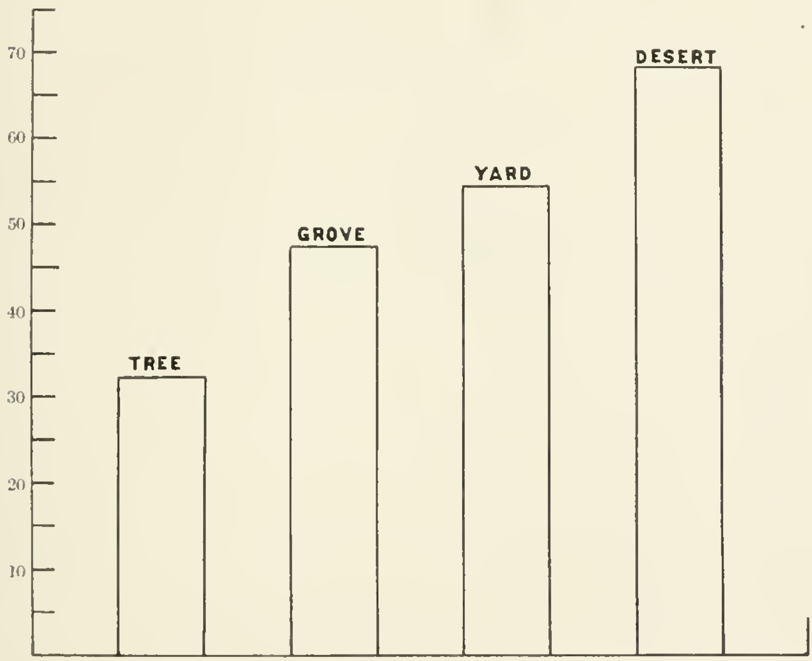

Fig. 3. Comparison of the average daily atmometer water loss from the stations referred to in figure 2.

ing something of the relative harshness of the two seasons, both as reflected in the amount of dropping and in the data taken by the U. S. Weather Bureau observer at Bakersfield, we are able to approximate fairly well the climatic conditions at Edison in 1917 for comparative purposes. The water loss from our different stations at the two localities is well shown in figures 2, 3, 4, and 5 and in table 5.

At Edison our atmometer stations were selected as follows: "Tree" station was located underneath an orange tree near the center of the orchard, about one-half mile to leeward of the edge of the orchard

[47] The Relation of Desert Plants to Soil Moisture and to Evaporation, Carnegie Inst. Washington, Publ. 50, 1906.

[48] Comparison of the Hourly Evaporation Rate of Atmometers and Free Water Surfaces with the Transpiration Rate of *Medicago sativa*, Jour. Agr. Res., vol. 9 (1917), pp. 277–96.

which bordered the desert. "Grove" station was situated in the open orchard midway between the tree just mentioned and its neighbor. "Desert" station was located on the open, bare desert about one-half

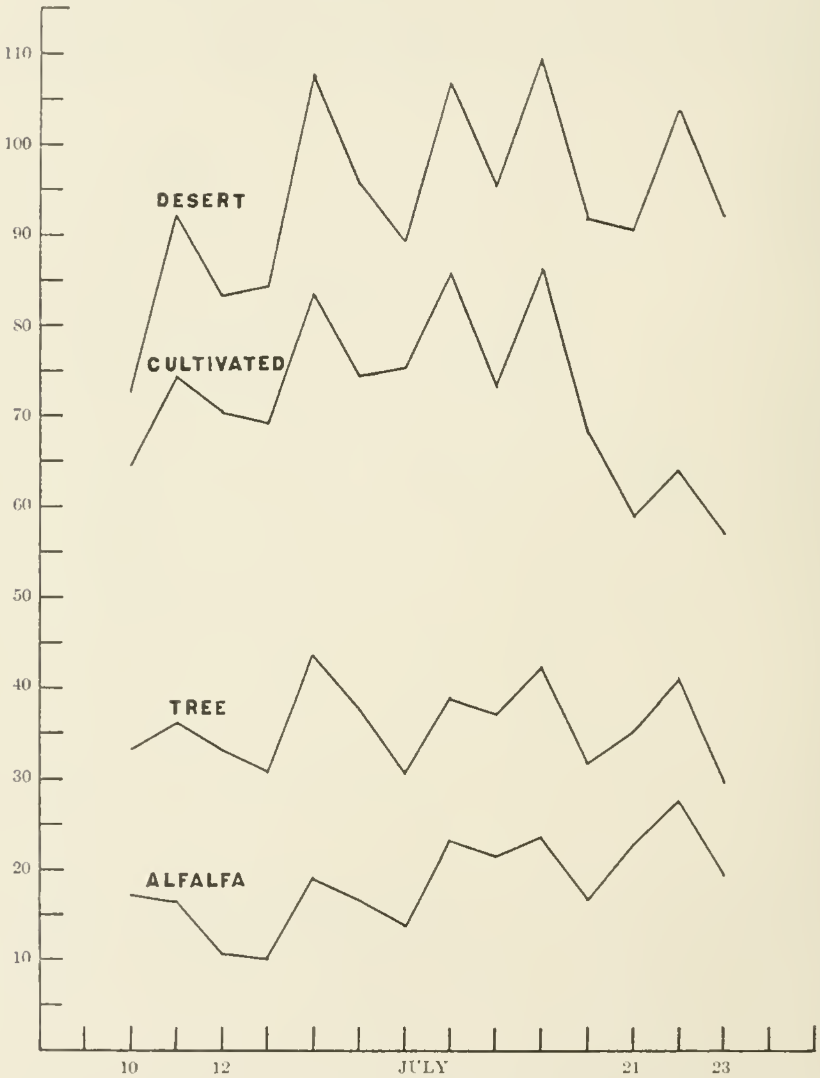

Fig. 4. Daily evaporation from atmometers at four different stations at East Bakersfield in 1917. Ordinates, water loss in cc.; abscissae, days of the month.

mile to windward of the edge of the orchard and many miles to leeward of any irrigated land (pl. 41)). The data accumulated for nineteen days are shown in figures 2 and 3 and table 5.

At East Bakersfield our atmometers were set up at the following stations: "Tree" station was similar to "Tree" station at Edison except that the tree where it was located was in the orchard planted to alfalfa. "Alfalfa" station was located similarly to "Grove" station at Edison but of course was surrounded on all sides by alfalfa,

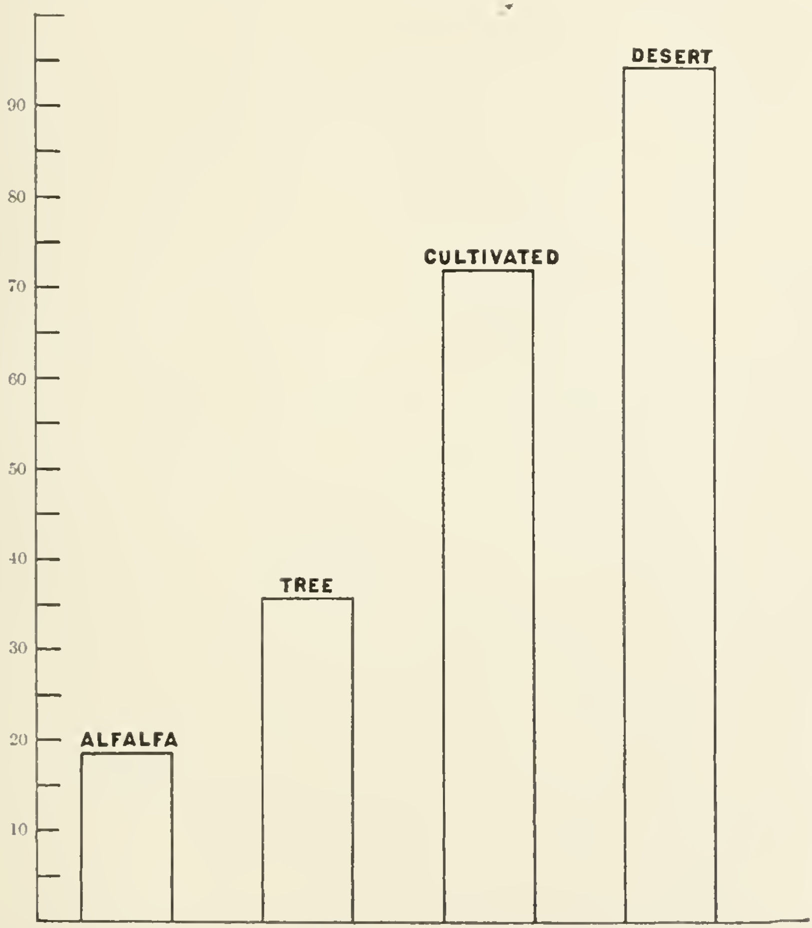

Fig. 5. Average daily water loss from atmometers at the stations referred to in figure 4.

which averaged some twelve to eighteen inches high. "Cultivated" station was located in every respect similarly to "Grove" station at Edison and the two "Desert" stations were similarly situated. The data accumulated for fourteen days are shown in figures 4 and 5 and table 5.

It is at once obvious, looking at the stations, which are in every way comparable, that the critical period in 1917 was considerably more severe than in 1916 (fig. 6), which difference has been pointed out with respect to the yield of the Edison orchard. It is also equally evident that the water loss from the soil and plants has a most profound effect in ameliorating the atmospheric evaporating power and that this effect is cumulative with the direction of the prevailing winds. Thus at Edison the "Desert" atmometer lost an average of 69.1 cc. to 48.1 cc. lost by the "Grove" station and at East Bakersfield the same stations lost water in the ratio of 94.0 cc. to 71.7 cc. At Edison the orchard environment during 1916 was sufficient to cut down the asperity of the climate about 45 per cent, while at the Kellogg place in 1917 it was sufficient to reduce it 31 per cent. The atmometer inside the tree lost only two-thirds of that lost by the instrument at "Grove" station or only 45 per cent of that at the "Desert" station. Thus we can see the marked effect of an orchard in modifying its own environmental complex. It is undoubtedy this influence which the orchard manifests *per se* which explains to some degree why it is that as orchards planted in exposed districts grow older, the percentage of yield increases more than the increase in size of tree. The fact that inside fruit is subjected to an entirely different climate than exposed fruit serves to explain why it is notably of better texture and grade and why it possesses so few large and protuberant navels. We have observed that Navel oranges grown in the University of California greenhouses are of markedly superior texture and navel conformation to those produced outside, where conditions are not so mild or uniform. Again, it is this cumulative modification of the climatic complex following the direction of the prevailing wind which explains the fact that a notably heavier set of fruit occurs on the south and east side of the trees. This condition has been frequently mentioned and was quite marked at Edison in 1917.

But the most striking modifications in climatic conditions are to be seen with reference to the situation at East Bakersfield. Although the Desert station atmometer lost an average of 94.0 cc. the Alfalfa station instrument lost only 18.5 cc. or only 20 per cent as much. Reference to table 5 serves to show that here is a climatic change within a half mile in the San Joaquin desert of the same magnitude as that between Miami, Florida, and Tucson, Arizona. The effect is, of course, largely due to the fact that the alfalfa transpires at a tremendous rate and the atmometer cup at that station was continuously bathed in an

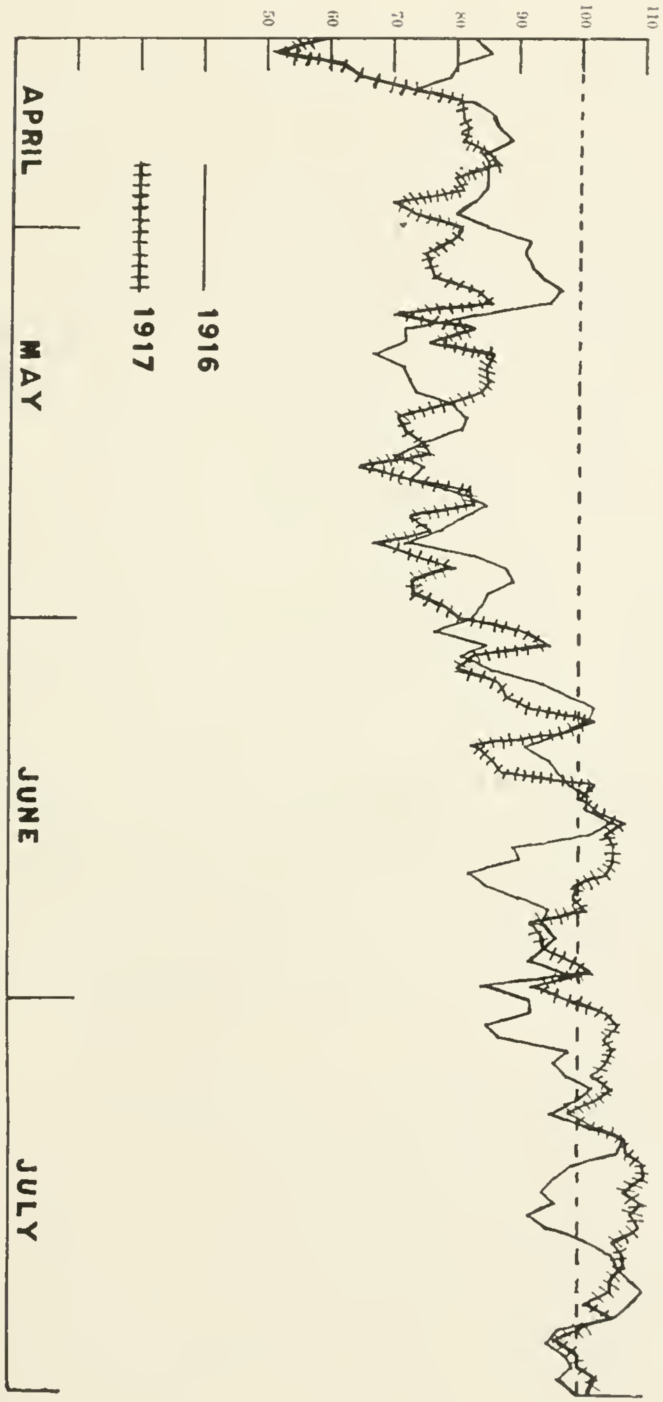

Fig. 6. Maximum daily temperatures for period April 15 to August 1, 1916 and 1917.

almost saturated atmosphere. The windbreak served to prevent the blanket of moist air from being rapidly dissipated. The loss from Tree station is seen to be 35.8 cc., or only 30 per cent of that lost by the Desert instrument. Although the effect of the alfalfa cannot be exerted at any very considerable height above the ground, still it is certain that the orange trees (with the young developing fruits) surrounded by this transpiring alfalfa are literally bathed in a damp atmosphere; at any rate so far as the tree is concerned it is subjected to a very different climate from that which obtains on the desert. The influence of the alfalfa in modifying the atmospheric humidity can clearly be seen when the crop of oranges is picked, for under these conditions most of the fruit is borne near the ground and less in the tops of the trees. At Tree station, East Bakersfield, thermo-hygrograph readings were taken for a period of twenty days. A study of the record for the period of the investigation shows some interesting results. At no time did the temperature rise above 107° F although in the laboratory, a quarter of a mile away, temperatures of 110° to 112° F were registered several times. The most significant feature, however, is the relative humidity curve. The lowest humidity reached was 25 per cent, which occurred at the time that the 107° F temperatures were recorded, July 9 and 21. The average relative humidity during the day was between 40 and 50 per cent. In 1916 at Edison we recorded humidities as low as 10 per cent and the average relative humidity was between 25 and 35 per cent. It is unfortunate that we were not able to obtain simultaneous temperature and humidity readings at the Desert station in 1917, but in view of the fact that the 1917 season has been shown to be much more severe than the 1916 season there is little doubt that in 1917 the relative humidity was somewhat lower and the temperature somewhat higher than in the former season.

We recognize clearly that in agricultural enterprises it is unsafe to rely upon climatic averages. It is well known that with some crops success or failure depends largely upon the extremes of climatic conditions experienced during a certain critical period in their growth. However, it should be borne in mind that conditions which tend to ameliorate the environmental complex not only raise the general average favorably, but also have a distinct modifying effect upon extremes in weather conditions which may occur. Indeed, it seems probable that this is the most important effect of the alfalfa and windbreaks in the Kellogg orchard. It is not so much the higher

average humidity as it is the greater freedom from extreme variation in climatic conditions which serves to enable the young fruits to survive.

As referred to above, the junior author[49] has shown in another place that a marked water deficit occurs both in the young fruits and the leaves under the climatic conditions obtaining at Edison and has suggested that these abnormal water relations furnish the stimulus to abscission. If this be so, then when there is little or no dropping of the fruits and consequently a good crop, such abnormal water relations should not be found. An effort was made at the East Bakersfield station in 1917 to establish such abnormal water relations, but it was found impossible to do so (table 8). Instead of there being a regular

TABLE 8

AVERAGE MOISTURE CONTENT AT DIFFERENT TIMES OF DAY

Kind of material	Average water content in per cent, calculated on basis of dry weight 1916	1917
Normal fruits one-third to three-fourths inch in diameter gathered before noon	260.2	285.3
Same, but gathered after noon	247.0	283.9
Leaves of current season's growth, gathered before noon	164.9	174.9
Same, but gathered after noon	157.2	182.6

decrease in water content of similar leaves and fruits during the day, which is made up during the night, no such relation was found. At East Bakersfield the leaves and fruits, in the first place, averaged somewhat higher in moisture content than those taken at Edison. Secondly, although as nearly similar in every respect as possible, duplicate series showed an absolute lack of uniformity, the variation sometimes being as much as 30 to 40 per cent. Finally, no average decrease in water content either of the fruits or leaves was found to occur during the day. It should be mentioned that irrigation at the Kellogg place is not uniform, relatively small tracts being irrigated at one time and these thoroughly soaked. As it was found inconvenient to take all the leaves and fruits from the same trees it is possible that some of the variation in moisture content noted may be attributed to variations in soil moisture. However, under the marked modification of climatic conditions which has been shown to occur as a result of the management of the orchard, it is believed that such abnormal water relations do not occur, at least to anything like the extent to which they do under the unmodified climatic conditions.

[49] *Loc. cit.*

As to the ultimate stimulus beyond abnormal water relations we can do little but speculate. Lloyd[50] has expressed the idea that increase in temperature following water deficits may be the ultimate stimulus to abscission. It has long been known that plant parts, when for any reason deprived of a normal supply of water, suffer an increase in internal temperature. In an effort to furnish additional evidence as to the presence of abnormal water relations, as well as to obtain some idea of the temperature changes incident to such water deficits, we took some temperatures of fruits destined to fall, fruits suffering from a water deficit by reason of the fact that the tree was permitted to suffer for lack of irrigation, and temperatures of normal fruits. These are found summarized in tables 9 and 10. It will be seen that

TABLE 9

INTERIOR TEMPERATURES OF FRUITS, FAHRENHEIT

Hour	Fruit destined to drop	Normal healthy fruit	Air
9	91.8	91.4	91.5
9:20	94.1	91.5	93.2
10	96.3	93.0	95.9
11	100.4	96.9	97.5
12	102.2	98.0	100.4
1	106.5	100.9	105.8
2	110.5	104.9	110.1
3	109.9	107.2	109.0
4	111.9	110.3	110.8
5	111.2	110.3	107.2
5:30	107.6	107.6	106.2
Average	103.8	101.0	101.6

TABLE 10

INTERIOR TEMPERATURES OF FRUITS, FAHRENHEIT

Hour	Fruit suffering from drought	Normal healthy fruit	Air
8	87.3	86.9	90.1
9	91.4	90.5	92.1
10	95.5	95.0	97.5
11	98.6	97.2	100.2
12	102.9	100.4	103.6
1	104.2	103.5	105.2
2	104.9	104.0	107.6
3	106.2	105.8	107.6
4	104.0	104.0	104.0
5	101.3	101.3	101.6
6	98.6	98.6	98.2
7	93.2	93.2	94.1
Average	99.0	98.2	100.1

[50] *Loc. cit.*

the normal fruits average somewhat lower in temperature than the air, and in turn those destined to drop are somewhat higher in temperature than the air. Fruits permitted to suffer for lack of water show a temperature approximately that of the air surrounding them. It may be that increase in temperature due to water deficits is the ultimate stimulus to abscission, still it should be pointed out that the increases in temperature as recorded by us are of a much smaller magnitude than the daily range in temperature changes. We are fully aware, of course, that strictly accurate temperatures of plant tissues can only be obtained by thermo-electric means, the mercury thermometer being too subject to fluctuation and variation for very delicate work.

Factors Operative in Causing Water Relation Strains

It is of course obvious that, given a plant transpiring a certain amount of water vapor daily, unless there be a sufficient water supply in the soil within reach of the absorbing roots to make up for that lost by the plant and in addition supply enough for its metabolic processes, water deficits of the kind mentioned must eventually occur. That under these conditions such do occur and that they are followed by an abnormally severe shedding of the young fruits when in the critical period, is the observation of the authors and the experience of many growers. In the season of 1916 the junior author had under observation a ten-acre block of orange trees in the Oroville district which had been top worked to the Washington Navel variety five years previously. They bloomed very heavily and set an excellent crop. Through an accident to the irrigation system preventing a sufficient supply of water these trees were allowed to suffer for lack of water at the time when the young fruits were about one centimeter in diameter. At the time of irrigation several days later the fruits had not fallen and it was hoped that the crop could be saved. Within a week practically every fruit was shed, although the trees looked well and had entirely recovered from the drought.

Observations, confirmatory in every respect to those given above, were made on a row of trees at the Kellogg place in 1917. These trees were permitted to suffer for lack of irrigation. Although the only trees in the row which at the time bore fruits in the critical stage were of the Valencia variety, which variety is much less subject to shedding than the Washington Navel, still within a week after the application of the water many of the young fruits had fallen. The desirability of

a proper moisture supply in the soil at the blooming and setting period is reflected in the practice of many growers who irrigate their orchards heavily at such times as well as during the periods of hot, dry north winds.

In this connection it should be noted that Fowler and Lipman[51] have recently shown that under conditions of a soil moisture supply somewhat below the optimum the visible effects upon the citrus tree are a great deal less than under conditions of the same percentage above the optimum moisture content. In other words, these authors have shown that the citrus tree does not exhibit the effects of a deficient soil moisture supply to the same extent that it does an excess of moisture in the soil. It may well be, therefore, that many of our citrus orchards are underirrigated and the irregular water relations above discussed accentuated by reason of this fact. The authors feel that many of the orchards studied in this investigation would probably do better with heavier irrigation. Manifestly it would be useless to attempt methods of modifying the climatic complex with the end in view of cutting down daily water deficits, if the soil moisture supply is deficient. Therefore, the grower should first make certain that sufficient soil moisture is available.

It has long been known that the presence of sufficient moisture in the soil is not conclusive evidence that the plant is enjoying optimum moisture conditions. Plants inhabiting salt marsh regions possess their xerophytic adaptations by reason of the fact that although growing with their roots in water or mud they are unable to obtain water in any large amounts and are forced to economy in the use of it. This inability to absorb water has been traced to the ratio between the osmotic concentrations of the soil solution and the cell sap of the roots, and such a condition is called "physiological drought." Physiological drought may be induced by the inhibition of absorption through the action of factors other than the osmotic concentration of the solutions involved.

Among the most important factors conditioning absorption is that of aeration. It has long been known that when grown in water cultures many plants make very unsatisfactory growth. Hall, Brenchley, and Underwood[52] have recently shown that this unsatisfactory growth is due to lack of aeration and can be remedied by passing a stream of

[51] Optimum Moisture Conditions for Young Lemon Trees on a Loam Soil, Univ. Calif. Publ. Agr. Sci., vol. 3 (1917), pp. 25–36.

[52] The Soil Solution and the Mineral Constituents of the Soil, Jour. Agr. Sci., vol. 6 (1914), pp. 296–301.

air through the solution. The economic applications of this principle are many, but are of course particularly evident in regions where through special conditions lack of soil aeration is emphasized, as is the case in certain parts of India. The soil is naturally very heavy and easily packed by the torrential rains. Lack of aeration is accentuated during certain portions of the growing season by the occurrence of monsoons and tropical rainstorms of great severity. Howard[53] has shown most conclusively that under these conditions the production of the gram or chick-pea, *Cicer arietinum*, grown to the extent of over eighteen million acres, is absolutely conditioned by the soil aeration. If the soil is permitted to become packed by summer rains and the air supply cut off, the plants wilt down with water actually standing on the surface of the soil. Absorption is cut down to practically nothing, while transpiration is not reduced in the same ratio, resulting in ultimate wilting. While not extensive, all the experimental data available on the production of this crop in California show this same intolerance of lack of soil air. Howard has shown this same condition affecting fruit trees and other crops, among which is the indigo plant. Free[54] has shown that with *Coleus blumei* "even a very small decrease of oxygen below that normal to the atmosphere is injurious to the plant. Thus a plant, the roots of which were supplied with gas consisting of 75 per cent air and 25 per cent nitrogen, was injured within three days and killed within 45 days. With lower oxygen content in the soil atmosphere injury and death are still more prompt." In many cases the lack of aeration is first evidenced by the shedding of the leaves and flowers. Soils of arid regions in general are well aerated, and especially soils of open structure such as sands and sandy loams. Therefore it is not likely that lack of soil aeration is the factor conditioning absorption of water by citrus trees. However, this problem is now under investigation and will be reported on later.

Under most conditions of lack of aeration not only is oxygen deficient but carbon dioxide is present in excess. The experimental data available seem to indicate that while in general lack of oxygen and excess of carbon dioxide in the soil atmosphere are detrimental, there is no set rule. Cannon,[55] and Livingston and Free[56] have shown

[53] Soil Aeration in Agriculture, Agr. Res. Inst. Pusa, Bull. 61, 1916.

[54] Cannon, W. A., and Free, E. E., The Ecological Significance of Soil Aeration, Science, n.s. vol. 45 (1917), pp. 178–80.

[55] On the Relation between the Rate of Root-Growth and the Oxygen of the Soil, Ann. Rep. Dir. Dept. Bot. Res., Carnegie Inst. Washington, Yearbook 15 (1916), pp. 74–75.

[56] Relation of Soil Aeration to Plant-Growth, *ibid.*, p. 78.

that there is considerable variation in this respect, some plants, such as *Salix* sp., growing and thriving in a soil containing no oxygen. Apparently the limiting concentrations of these gases must be worked out for each plant separately. As to the specific effect of lack of oxygen and excess of carbon dioxide resulting in changes in absorption rate little is definitely known. The first effect seems to be a slowing down of growth, which in turn being ordinarily accompanied by the imbibition (in the case of the embryonic growing regions of the root) of water in considerable amounts, reduces absorption markedly. The exact relation between growth and absorption is not well understood at the present time; but it has been shown by MacDougal[57] and others of the Carnegie Institution that growth of embryonic tissues is mainly accomplished by the imbibition of large quantities of water. It can be readily seen, therefore, that if conditions are unfavorable for growth, imbibition and absorption must necessarily be reduced.

Another factor which acts in a very similar way to lack of aeration, and one little appreciated up to the present time, is that of soil temperature. Every year adds more confirmatory evidence to prove that the temperature relations of physiological processes follow certain typical curves, which seem to be identical or closely related for processes of the same fundamental nature in different organisms. The effects of temperature on physiological processes, both in plants and animals, have been investigated by many workers and in general a modified curve of the Van 't Hoff type has been obtained where the most careful work has been done. In such curves several cardinal points can be determined, namely, the minimum temperature at which the process goes on, the maximum temperature beyond which the process no longer continues, and the optimum temperature at which the process is most active. This last term has been superseded by what is known as the maximum rate temperature, representing that temperature above which the rate is ultimately decreased and below which the same occurs. Blackman[58] has shown that the term optimum temperature is indefinite, since at certain temperatures physiological processes are very rapid for a time but then slow down, due to the introduction of a time factor. The maximum rate temperature is that temperature above which a time factor is introduced resulting in an ultimate retardation of the process.

These cardinal temperatures differ somewhat for different processes but still more markedly do they differ for the same process in different

[57] *Ibid.*, Yearbook 15, 1916.

[58] Optima and Limiting Factors, Ann. Bot., vol. 19 (1905), pp. 281–95.

organisms. Thus Howard[59] has shown with wheat that at the germinating period a fall of 10° to 12° F from 84° to 72° may mean the difference between success and failure in obtaining a stand, since the growth rate is almost inhibited at the former temperature. On the other hand, Cannon[60] has shown that the maximum rate temperature for the mesquite, *Prosopis velutina*, and *Opuntia* is about 93° F. Tobacco is another plant which thrives in hot soils. Leitch[61] has shown that for the garden pea, *Pisum sativum*, 85° F is the maximum rate temperature and above 110° F no growth whatever occurs. Apparently, as in the case of the aeration factor, no general rule for these cardinal temperatures can be laid down. They must be determined for each plant separately. Since growth conditions absorption we are justified in assuming that the cardinal temperatures for growth are approximately those for absorption.

The genus *Citrus*, as mentioned elsewhere, is native to the tropics, where it grew in the shade of other trees. Under these conditions the soil was damp and soil temperatures certainly not high. It therefore seems logical to assume that the temperatures favorable for root growth in *Citrus* are not very high. As grown under clean cultivation in the arid southwest we believe that the absorbing roots are subjected during a certain portion of the day to temperatures above the optimum and that during such periods absorption is actually reduced.

TABLE 11

SOIL TEMPERATURES (F.) AT EDISON, JUNE 7, 1916

Hour	A.M. 9:15	10:15	11:15	P.M. 12:15	2:15	3:15	4:15	5:15
Six-inch dust mulch	80.6	84.2	88.2	92.3	94.1	96.0	99.5	99.0
First 6 inches	77.0	78.3	80.0	84.2	89.6	88.8	88.6	87.0
Second 6 inches	77.0	76.1	76.1	78.0	82.4	82.4	82.4	80.6
Third 6 inches	76.1	75.0	75.0	75.3	79.2	77.2	78.3	78.0
Fourth 6 inches	74.3	74.3	74.6	74.6	77.2	76.6	77.0	77.0
Six-inch dust mulch in shade of tree	71.6	73.6	74.3	81.0	83.7	82.5	82.2	82.2

To obtain an idea of the soil temperatures prevailing in the upper two feet of soil in 1916, a comparatively cool season, we made a series of hourly readings at six-inch intervals. These may be found summarized in table 11. This table shows that during the afternoon

[59] Influence of Weather on Yield of Wheat, Agr. Jour. India, vol. 2 (1916), part 4.

[60] Relation of the Rate of Root Growth in Seedlings of *Prosopis velutina* to the Temperature of the Soil, Plant World, vol. 20 (1917), pp. 320–33.

[61] Some Experiments on the Influence of Temperature on the Rate of Growth in *Pisum sativum*, Ann. Bot., vol. 30 (1916), pp. 25–46.

the temperature of this upper layer of soil does not fall below 75° F. As was brought out previously, under clean cultivation practices the absorbing roots of citrus trees are largely located in the upper two feet of soil (pl. 42). It therefore seems quite probable that during the afternoon at the very period when water loss by transpiration is greatest, absorption is inhibited by high soil temperatures. A study of the cardinal temperatures for absorption by citrus roots, which is expected to throw considerable light on this question, is now under way and will be reported on later.

But granted that a condition of physiological drought existed, due to the action of the factors just discussed, still the citrus tree might

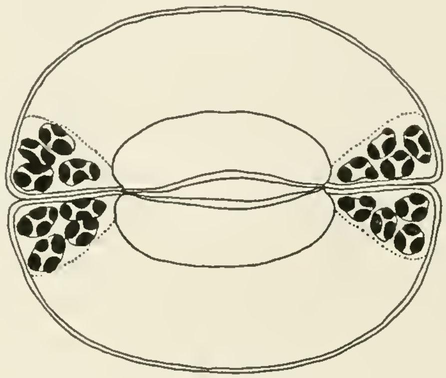

Fig. 7. Citrus stoma showing maximum opening. From orange leaf just reaching full size.

maintain itself in a proper water balance were it not for the fact that it is not provided with efficient means of conserving its water by regulating its loss through transpiration. A preliminary study of the relation of cuticular transpiration to stomatal water loss has brought out the fact that from 40 to 50 per cent of the water loss from citrus leaves occurs through the upper epidermis which does not contain stomata. These studies have shown that the young leaves are more efficient than the older leaves but that even the youngest leaves lose as much as 25 per cent of their water through the upper epidermis.

A study of the stomatal condition in citrus leaves has brought out some interesting facts. By the use of Lloyd's method[62] the amplitude of stomatal movement was studied. It was found that very early in the life of the leaf the stomata lose their power of opening and closing and remain practically closed thereafter (fig. 7). In some cases the

[62] Physiology of Stomata, Carnegie Inst. Washington, Publ. 82 (1908), p. 26.

closure is not complete and the stomata remain slightly open. Heilbronn[63] has established this same condition in the leaves of the *Camelia*. It is interesting to note in this regard the results obtained by Shreve[64] in a study of the transpiration of rain-forest plants carried on in Jamaica.

> The true stomatal transpiration is thus found to be from 42 to 48 per cent of the total water-loss of the leaf. The close relation of transpirational behavior to evaporation is thus shown to have its basis in the fact that rather more than half of the water-loss of the plant goes on through the epidermal surfaces. . . . The amplitude of stomatal movement in rain-forest plants under shade conditions has been found to be relatively small. . . . The weakness of the movements, together with the high cuticular water-loss, serves to give the stomata a very negligible rôle as regulators of transpiration rate, particularly during the daylight hours.

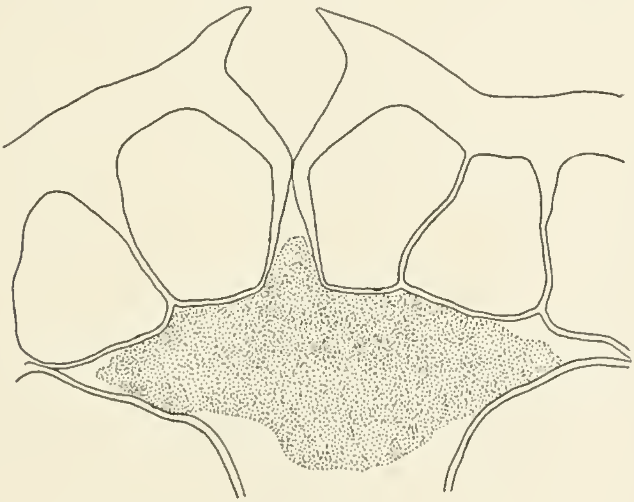

Fig. 8. Cross-section of stoma from old coriaceous orange leaf. Note resinous deposit in the substomatal cavity.

It was found that a varying percentage of citrus stomata are occluded by deposits of a resinous, gummy nature (fig. 8) in the substomatal cavity. Haberlandt[65] points out that physiological degeneration of stomata takes place in a number of shade-loving hygrophytes, doubtless because members of these ecological classes never require much protection against excessive transpiration. Therefore it can be readily appreciated that the citrus plant has relatively little control

[63] Ber. d. deut. bot. Ges., vol. 34 (1916), pp. 22–31. (Cited from Exp. Sta. Record.)

[64] The Transpiration Behavior of Rain-forest Plants, Ann. Rep. Dept. Bot. Res., Carnegie Inst. Washington, Yearbook 12 (1913), pp. 74–76.

[65] Physiological Plant Anatomy (London MacMillan, 1914), p. 272.

over its water loss. This condition itself constitutes strong evidence of its tropical origin.

If there be any regulatory action upon transpiration it should be brought out in a study of the transpiration curve as compared to the evaporation curve. These two curves for a typical day in July are shown in figure 9, and it will be seen that the general form is very similar and that the maxima of the two were reached at the same

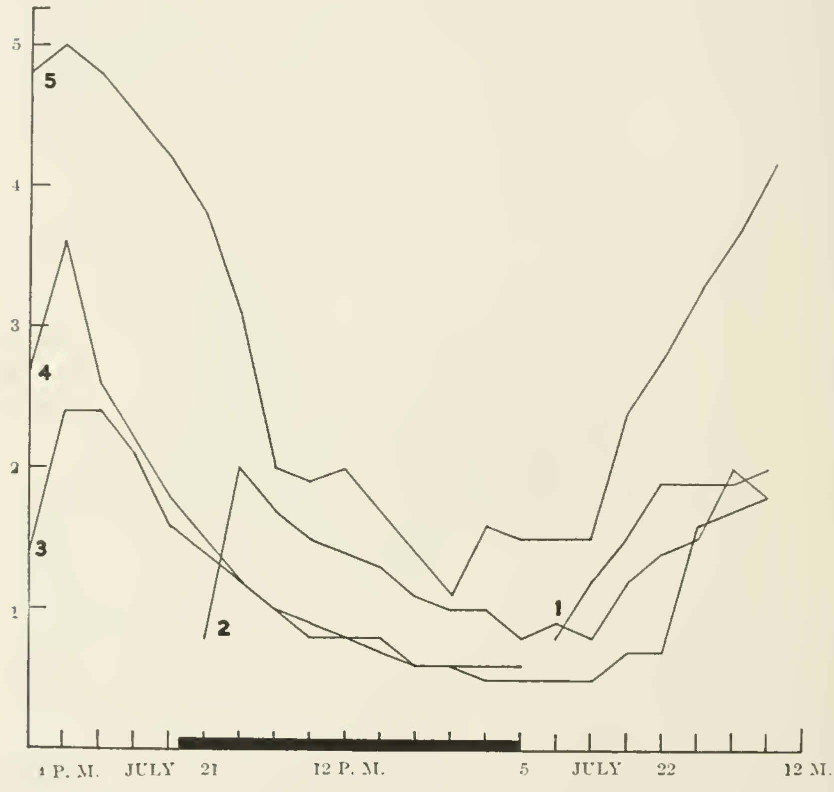

Fig. 9. Comparison of *Citrus* transpiration curves with the evaporation curve for the same period. Nos. 1, 2, 3, and 4 are transpiration curves obtained by the potometer method. No. 5 is the evaporation curve obtained from a Livingston white cylindrical porous cup atmometer. Ordinates represent water loss in cc.; abscissae, hours of the day.

period. Were there any regulatory action the transpiration curve should reach its maximum some time before the evaporation curve.

Susceptibility of Citrus Varieties to Abscission

It is well known that when grown under similar conditions the Valencia variety of orange and the pomelo do not shed the young fruits in anything like the same proportion as the Washington Navel.

If the stimulus leading to abscission be abnormal water relations, why then do not these two other members of the genus shed their fruits to the same extent as the navel variety? Our observations made in the field in orchards where these varieties are mixed have shown that such is not the case, and experiments performed in our laboratories have shown that abscission is much more easily induced in the navel variety than in the others. Shoots bearing flowers and young fruits of each variety have been placed in moist chambers and kept at room temperature. In the case of the navel variety abscission of all the flowers and fruits has invariably occurred within sixty hours, while in the Valencia variety and with lemons frequently no abscission occurred within five to eight days. Apparently the navel variety is much more susceptible to stimuli which lead to abscission. In this connection it seems desirable to call attention to the fact that other investigators have found in the case of hybrids abscission is much more prevalent and much more easily brought about than in the case of the parent varieties. Thus Goodspeed and Kendall[66] have shown that in the case of certain tobacco crosses in which only a small proportion of the ovules are normally matured and capable of fertilization, which condition obtains in the navel orange variety, practically all the flowers and young fruits are abscissed. May not this sensitiveness to stimuli which cause abscission constitute further evidence that the Washington Navel variety is of hybrid origin?

Methods of Amelioration

From the preceding discussion it is obvious that all methods of preventing the June drop of our present strains of Washington Navel oranges must be in the nature of modifying the environmental complex either above ground, below ground, or, as is usually the case, both.

If the cause underlying these water deficits lies in the asperity of the atmospheric complex then practices tending to ameliorate climatic conditions should work out to produce heavier crops. Such has been found to be the case. The planting of windbreaks to prevent the dissipation of blankets of moist air; a moderate winter pruning to reduce the total leaf surface area; and the planting of intercrops, such as alfalfa, sweet clover, or buckwheat, which transpire large amounts of water vapor; all these are methods of modifying the atmospheric environmental complex.

[66] On the Partial Sterility of *Nicotiana* Hybrids made with *N. sylvestris* as a Parent, III: An Account of the Mode of Floral Abscission in the F_1 Species Hybrids, Univ. Calif. Publ. Bot., vol. 5 (1916), pp. 293–99.

In this connection it should be emphasized that the beneficial effect of a summer cover crop does not seem to be due so much to the raising of the average humidity as it does to the buffer effect which it plays when sudden extremes in climatic conditions are experienced. The increase in the average humidity occasioned by the use of a summer cover crop is probably considerably smaller than the difference which may exist from one season to the next. It does not seem so important that the average humidity has been increased somewhat by its use as that when sudden hot, dry spells are experienced their effect is modified by the use of such a crop. This would seem also to explain the effect of the straw mulch which of course does not affect the atmospheric humidity to any extent.

If the limiting factor causing these abnormal water relations be high soil temperatures then methods of orchard management which will reduce such temperatures may be expected to result in heavier crops. Such practices as mulching and the growing of intercrops are known to reduce the soil temperatures. Moreover, such practices in many cases have resulted in notably heavier yields. The junior author had under observation a twenty-acre orchard in the Oroville district in the 1917 season. This tract was planted out to purple vetch in the late fall and was not plowed until the following June. It was heavily irrigated during April and May. Although situated in a most exposed position this orchard bore a much better crop than any other orchard in this district, notwithstanding the extremely heavy fall of fruits experienced in this season. It is possible that the heavy crops borne at the Kellogg place are partly attributable to a reduction in soil temperature during the growing season.

Some data have been published on the effect of straw mulches on the setting of Navel oranges. Briggs, Jensen, and McLane[67] report as follows:

> The set of fruit was very light throughout the Riverside district in 1915, owing apparently to cold weather following the bloom. In the Sunny Mountain tract, where the mulched basins were first installed in 1913, the average number of oranges per tree on the check trees in 1915 was 116, while on the mulched-basin trees the average number of oranges per tree was 281, or two and one half times as many as on the check trees.

Similar results are reported from other tracts. It should be remembered, however, that the trees used in this work were not healthy but were badly mottled, and the increased setting may be attributable to

[67] The Mulched-Basin System of Irrigated Citrus Culture, U. S. Dept. Agr., Bull. 499 (1917), p. 30.

their improved health brought about by better soil moisture and humus conditions as well as improved temperature conditions. It has not yet been satisfactorily shown that the mulched-basin system alone will reduce the amount of drop on healthy trees, although in the light of the discussion above we believe it probable.

The determination of the specific factor, if it be a single factor, which produces the abnormal water relations established, is yet to be made. It is hoped that investigations planned for the coming season may aid in solving this question. The orchard management practices described above which result in heavier crops, unfortunately for investigational purposes, involve the modification of both the aboveground and under-ground environmental complex.

The fact that by proper means man is able to change the climatic conditions from those obtaining at Tucson, Arizona, to those at Miami, Florida, within the space of a half mile, augurs well for the successful control of the June drop. Measures of an anticipatory nature lie in the proper selection of the site before planting. The exposure to prevailing winds, the nearness to large irrigated tracts, the possibility of planting windbreaks; all these should be considered in the selection of a site for a Navel orange grove. Growers should accustom themselves to thinking of climate not in terms of great valleys and states but in strictly local terms. As has been pointed out above, the judicious selection of the site, coupled with proper methods of orchard practice, make it possible to secure marked modifications in our arid climate. The question of the advisability of the measures suggested is purely one of farm economics and does not lie within the province of this paper.

In view of the relatively small amount of shedding which is connected with the *Alternaria* fungus alone and because of the peculiar manner of infection the authors are led to believe that spraying with fungicides for the June drop will hardly pay for the materials and labor involved.

Another promising line of investigation looking toward control of the June drop lies in the selection and propagation of dry heat resistant strains of the Washington Navel variety. This variety, it is well known, is constantly throwing off bud sports or mutations and it is entirely possible that mutations may arise which are less sensitive to abscission stimuli, but at the same time satisfactory otherwise. Every grower should be on the lookout for such strains.

SUMMARY

1. Citrus trees as grown in the interior valleys of the arid southwest are subject to an environment entirely abnormal to them in their natural habitat.

2. Moreover, the principal variety grown in these regions, the Washington Navel orange, is itself decidedly erratic and unstable.

3. Among other troubles incident to the abnormal climatic conditions is that heavy dropping of the young fruits, with consequent light crops, known popularly as the June drop.

4. A study of the shedding has established the fact that it constitutes true abscission, involving the separation of living cells along the plane of the middle lamellae.

5. Exhaustive investigations as to the stimulus or stimuli responsible for the abscission have narrowed them down to two: a fungus, *Alternaria citri* E. and P., and climatic conditions.

6. It is considered highly probable that a certain varying per cent of the drop, occurring relatively late in the season, is brought about by the stimulation of this fungus, which is also responsible for a black rot of those infected fruits which remain on the trees to maturity.

7. This fungus is of very wide distribution and infection of the young fruits is made possible through the peculiar structure of the navel orange.

8. The amount of infection is dependent upon weather conditions and the more or less fortuitous configuration of the navel end of the young fruits.

9. On account of the peculiar manner of infection and the relatively small amount of shedding due to the fungus, spraying will probably not pay for the labor and materials involved.

10. By far the greater part of the shedding, which occurs earlier in the season, is due to a stimulus to abscission arising from daily water deficits in the young developing fruits, resulting from the asperity of the climatic complex to which the trees are subject.

11. The principal factor in causing these abnormal water deficits lies in the fact that citrus trees are not adapted to withstanding the heavy water loss incident to the desert conditions under which they are grown. The amplitude of stomatal movement is small and cuticular transpiration very high.

12. It is further believed that under the prevalent clean cultivation practice, the soil temperatures during a part of the day are so high as

to result in the inhibition of absorption at the very time of day that water loss by transpiration is greatest.

13. It has been found possible to modify climatic conditions in an orchard so as to set crops in every way comparable with those produced in much more climatically favored citrus districts.

14. Under these modified climatic conditions the abnormal water relations referred to apparently do not occur.

15. Practical means of amelioration lie in heavier and more frequent irrigation, the planting of intercrops, mulching with straw and other materials, protection by means of windbreaks, and a reduction of leaf area by moderate winter pruning.

16. Measures of an anticipatory nature lie in the judicious selection of the site for the orchard with reference to its exposure, nearness to large irrigated bodies of land, and other features calculated to ameliorate climatic conditions.

17. Orchardists should be on the lookout for mutant strains which are dry heat resistant and satisfactory in other features.

This investigation had its inception with the senior author, who began the experimental work in March, 1916. In May, 1916, the junior author became connected with the Division of Citriculture and has been associated in the study of this problem ever since. Early in the investigation it became evident that there were at least two distinct promising lines of inquiry involved in the problem. The first, having to do with the relation of a certain almost ever-present fungus to the falling of the young fruits, is largely the work of the senior author. The second, having to do with the relation of the shedding to environmental conditions, although originating with the senior author and receiving constant study by him, constituted the main problem of the junior author, who moreover is responsible for the histological work involved in the investigation. The combination of attack, both on the pathological and physiological side, has given most satisfactory results and it is the belief of the authors that when investigated in a somewhat similar manner many of our so-called "physiological diseases" may be better understood.

The authors wish to ackowledge their indebtedness to Drs. F. E. Lloyd, W. A. Cannon, T. H. Goodspeed, and C. B. Lipman for suggestions and assistance, and to Mr. W. W. Worden and Dr. C. W. Kellogg for kindly coöperation in placing their orchard facilities at their disposal.

Transmitted January 17, 1918.

EXPLANATION OF PLATES

PLATE 25

The Navel orange orchard of the Edison Land and Water Company, where much of the experimental work was done.

PLATE 26

Part of the Kellogg orchard at East Bakersfield, showing heavy stand of alfalfa (just cut) between trees and also heavy crop of fruit. Photographed November 25, 1917.

PLATE 27

Typical Washington Navel tree in San Joaquin Valley, showing heavy bloom.

PLATE 28

Nearer view of same tree, showing details of heavy bloom.

PLATE 29

One branch with leaves removed, showing large number of buds produced.

PLATE 30

Typical abscissed fruits. Those to the right abscissed at the base of the pedicel, those to the left at the base of the ovary. The two in the center are healthy fruits picked from the tree for comparison.

PLATE 31

Small dead orange persisting though abscissed both at base of ovary and pedicel. Large fruit safely through both abscission periods. The dead style abscissed much earlier but was retained in position by the ragged nature of the break.

PLATE 32

The serious wounds produced by katydids which never result in abscission.

PLATE 33

Terminal and axillary fruits.

PLATE 34

Apical end of ovary of Navel orange just after the style has been shed. Enlarged 10 diameters. Notice the ragged condition of the stylar scar.

PLATE 35

Large late drops showing discolored area beneath the navel, caused by infection with *Alternaria citri*.

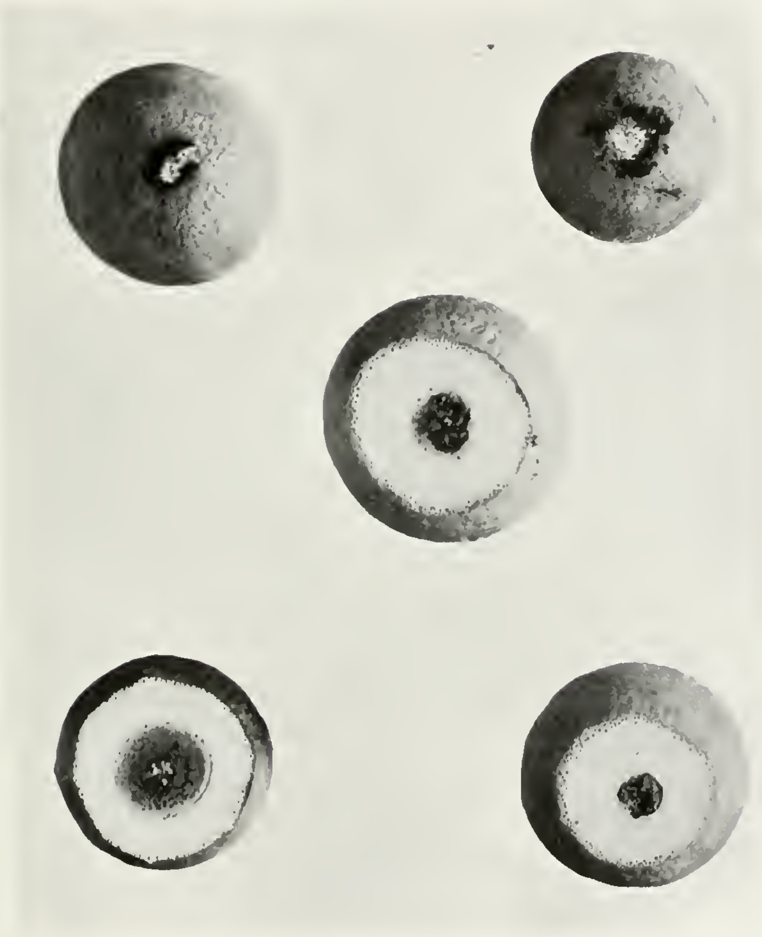

PLATE 36

Photomicrograph of *Alternaria citri*, showing the spores borne in long chains.

PLATE 37

Young Navel oranges, showing the ragged break of the style. Enlarged 2 diameters.

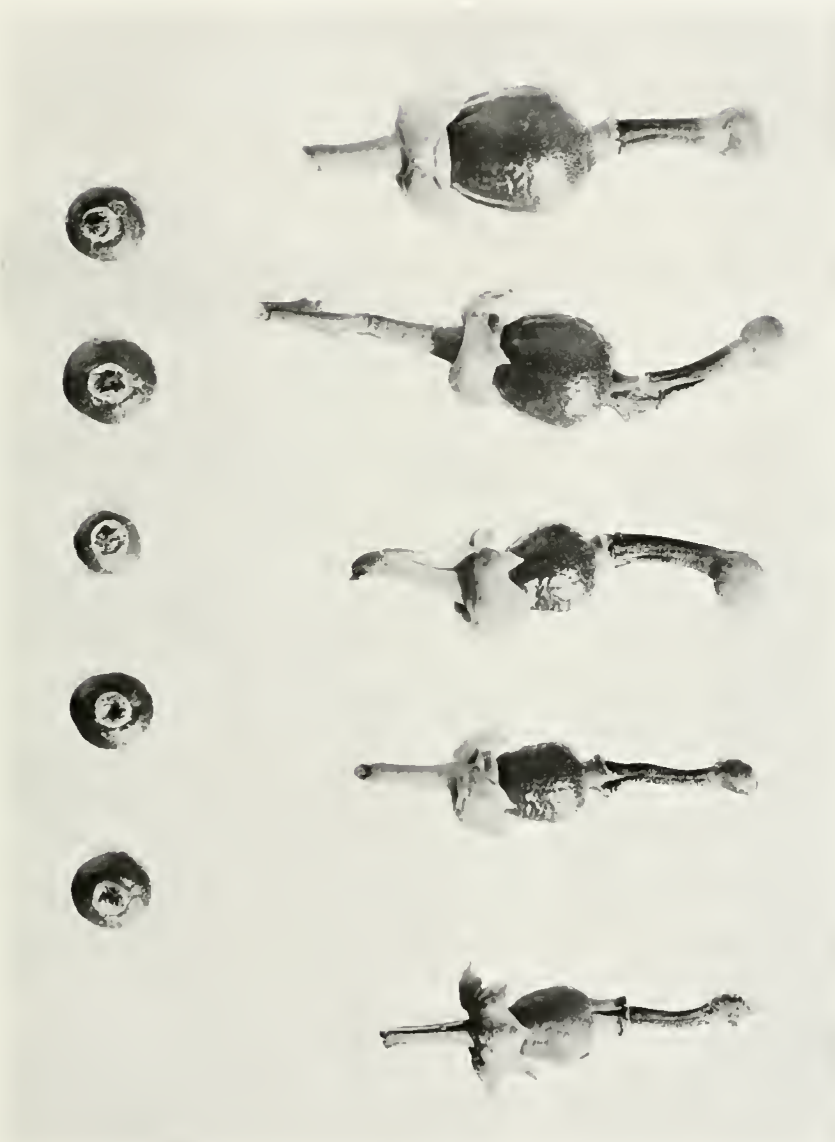

PLATE 38

Mummified oranges infected with *Alternaria citri*. Gathered under tree.

PLATE 39

Small Valencia orange, showing clean break between the base of the style and the ovary. Enlarged 10 diameters. Compare with plate 34.

PLATE 40

Showing the method of enclosing orange trees under the tents of cheesecloth in order that bees may be included in one and excluded from the other. The tree in foreground shows the method of covering inoculated flowers with paper sacks.

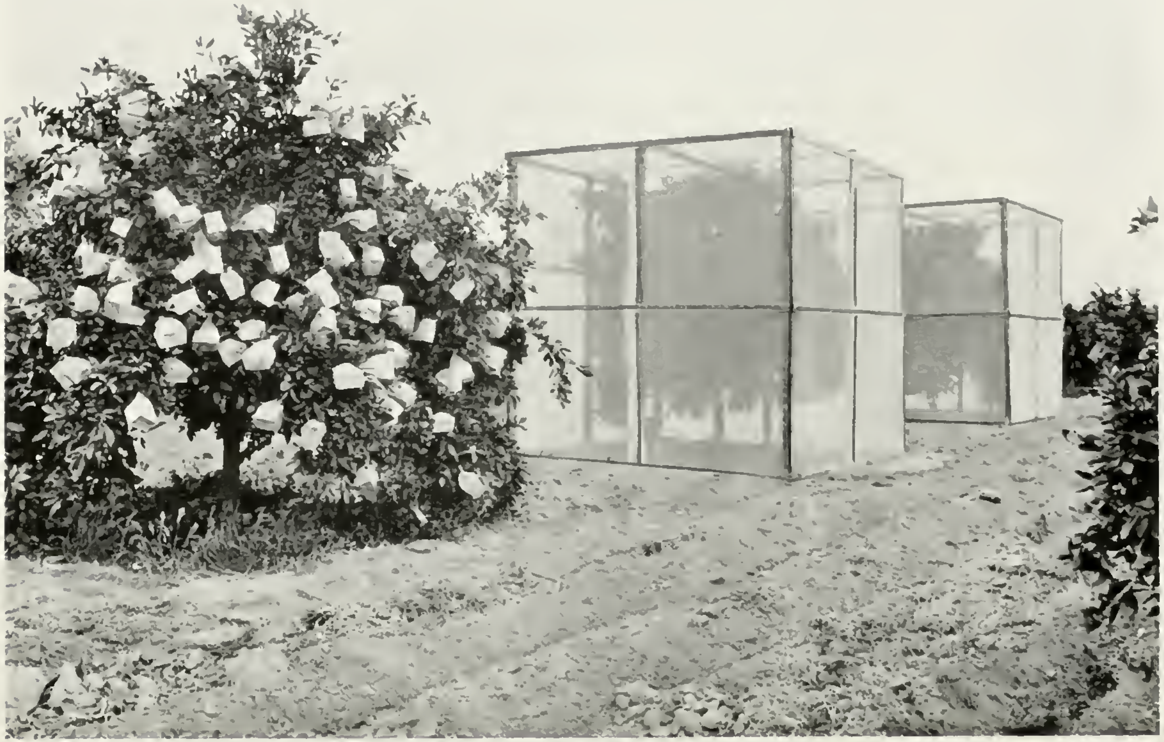

PLATE 41

The Livingston white porous cup atmometer as set up at our Desert station.

PLATE 42

Distribution of orange roots by six-inch layers at Edison station. Clean cultivation.


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